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Proceedings of the Third Biennial Conference of Research on the Colorado Plateau

Editors

Charles van Riper III
Elena T. Deshler

Third Biennial Conference of Research on
the Colorado Plateau
Northern Arizona University
Flagstaff

Sponsored and organized by
U.S. Geological Survey
Biological Resources Division

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Transactions and Proceedings Series NPS/NRNAU/NRTP-97/12
United States Department of the Interior
National Park Service
• 1997 •

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Contributors

Jason R. Bright
Sociology, Social Work and
Anthropology
Utah State University
Logan, Utah 84322-0730

Richard M. Bryant
National Park Service
Bryce Canyon National Park
Bryce Canyon, Utah 84717

William K. Carrel
Arizona Game and Fish
Department
Research Branch
2221 W. Greenway Road
Phoenix, Arizona 85023-4312

Arthur V. Chadwick
Southwestern Adventist University
Keene, Texas 76059

W. Wallace Covington
School of Forestry
Northern Arizona University
P.O. Box 15018
Flagstaff, Arizona 86011

Elena T. Deshler
USGS Biological Resources
Division
Colorado Plateau Field Station
Northern Arizona University
Box 5614
Flagstaff, Arizona 86011

James R. Ellenwood
USDA Forest Service
Kaibab National Forest
Williams, Arizona 86046

William B. Fawcett
Sociology, Social Work and
Anthropology
Utah State University
Logan, Utah 84322-0730

David L. Felley
415 East 25th Street
Cheyenne, Wyoming 82001

Dennis B. Fenn
USGS Biological Resources
Division
12201 Sunrise Valley Drive
Reston, Virginia 20192

Dan A. Foster
Nez Perce National Historic Park
Spalding, Idaho 83540

L. David Garrett
USGS Biological Resources
Division
Grand Canyon Monitoring and
Research Center
2255 N. Gemini Drive, Room 341
Flagstaff, Arizona 86001

Tim B. Graham
USGS Biological Resources
Division
Canyonlands National Park
Field Station
82 Dogwood Avenue
Moab, Utah 84532

Laura Grignon
Department of Botany
North Carolina State University
Raleigh, North Carolina 27695

Evan Hammer
Department of Geography
University of North Carolina
Chapel Hill, North Carolina 27514

Dennis D. Haywood
Arizona Game and Fish
Department
Research Branch
2221 W. Greenway Road
Phoenix, Arizona 85023

Ray Kablanow
Geological Technics, Inc.
2741 River Road
Modesto, California 95351

Elaine G. Kennedy
Geoscience Research Institute
Loma Linda University
Loma Linda, California 92350

Joy Nystrom Mast
Department of Geography and
Public Planning
Northern Arizona University
Box 15016
Flagstaff, Arizona 86011

Chris J. Mehling
USDA Forest Service
Chevelon Ranger District
HC 62, Box 600
Winslow, Arizona 86047

Theodore S. Melis
U.S. Geological Survey
1675 W. Anklam Road
Tucson, Arizona 85745

Jody P. Menzel
Department of Forestry
Northern Arizona University
Box 15018
Flagstaff, Arizona 86011

Vicky J. Meretsky
U.S. Fish and Wildlife Service
P.O. Box 338
Flagstaff, Arizona 86002-0338

C. Richard Miller
Arizona Game and Fish
Department, Region II
3500 S. Lake Mary Road
Flagstaff, Arizona 86001

Cheryl M. Mollohan
Arizona Game and Fish
Department
Education Branch
2221 W. Greenway Road
Phoenix, Arizona 85023

Richard A. Ockenfels
Arizona Game and Fish
Department
Research Branch
2221 W. Greenway Road
Phoenix, Arizona 85023-4312

Steven S. Rosenstock
Arizona Game and Fish
Department
Research Branch
2221 W. Greenway Road
Phoenix, Arizona 85023

Ronald J. Ryel
R. J. Ryel and Associates
1649 North 1000 East
North Logan, Utah 84321

Mark K. Sogge
USGS Biological Resources
Division
Colorado Plateau Field Station
Northern Arizona University
Box 5614
Flagstaff, Arizona 86011

Michael H. Soulen
Bureau of Reclamation
Grand Canyon Monitoring
and Research Center
2255 N. Gemini Drive, Room 341
Flagstaff, Arizona 86001

Richard A. Valdez
BIO/WEST, Inc.
1063 West 1400 North
Logan, Utah 84321

Charles van Riper III
USGS Biological Resources
Division
Colorado Plateau Field Station
Northern Arizona University
Box 5614
Flagstaff, Arizona 86011

Brian F. Wakeling
Arizona Game and Fish
Department
Research Branch
2221 W. Greenway Road
Phoenix, Arizona 85023

Gwendolyn Waring
School of Forestry
Northern Arizona University
P.O. Box 15018
Flagstaff, Arizona 86011

Brian Warren
Department of Geography
University of North Carolina
Chapel Hill, North Carolina 27514

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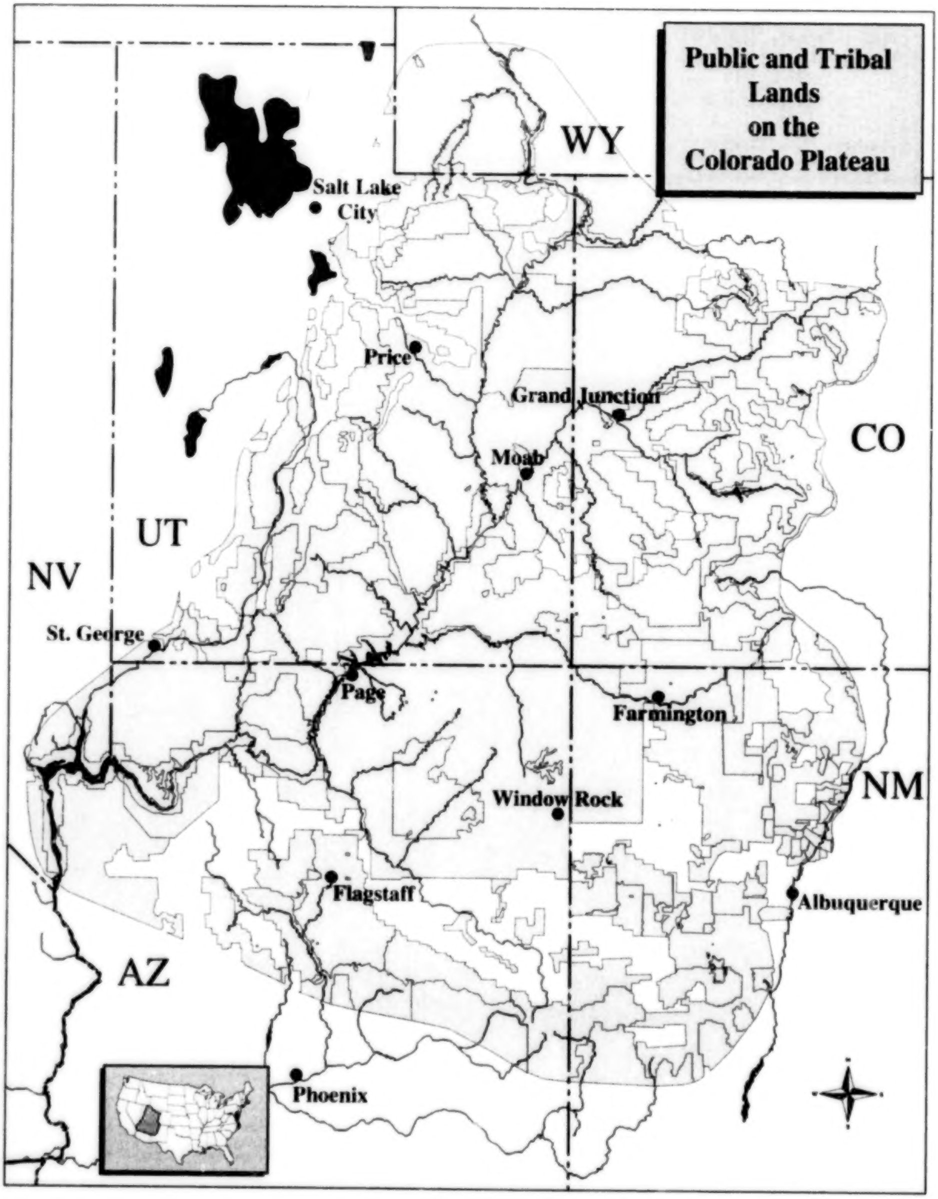
Preface

The papers in this volume are contributions from federal, state, and private sector researchers, who have come together to share scientific information with land managers on the Colorado Plateau. This Proceedings is the third in a series of publications that focuses on providing information to land managers on baseline scientific information pertaining to physical, cultural and biological resources of the Colorado Plateau. Support for these studies came from a spectrum of federal, state, and private partners concerned about the well-being of the Plateau's resources. I applaud the effort of the contributors. With modest funding and a broad base of public and institutional support, these authors have pursued important lines of work in the four states that comprise the Colorado Plateau biogeographic region.

There is much to be done. As a people, we face the prospect of extensive local land global environmental changes that continue to perturb the physical, cultural, and biological resources on our federal lands. As the research branch of the Department of the Interior, we in the USGS are committed to identify, in a sound scientific manner, information that can be used by land managers to protect our resources from detrimental change due to modern human influences. We must develop the information necessary to alert our managers, leaders, and our people to the importance of their natural surroundings as elements of those basic resources that sustain us, inspire us, and represent our natural biological and environmental heritage. Our task has just begun.

DENNIS B. FENN

U. S. Geological Survey
Biological Resources Division
Chief Biologist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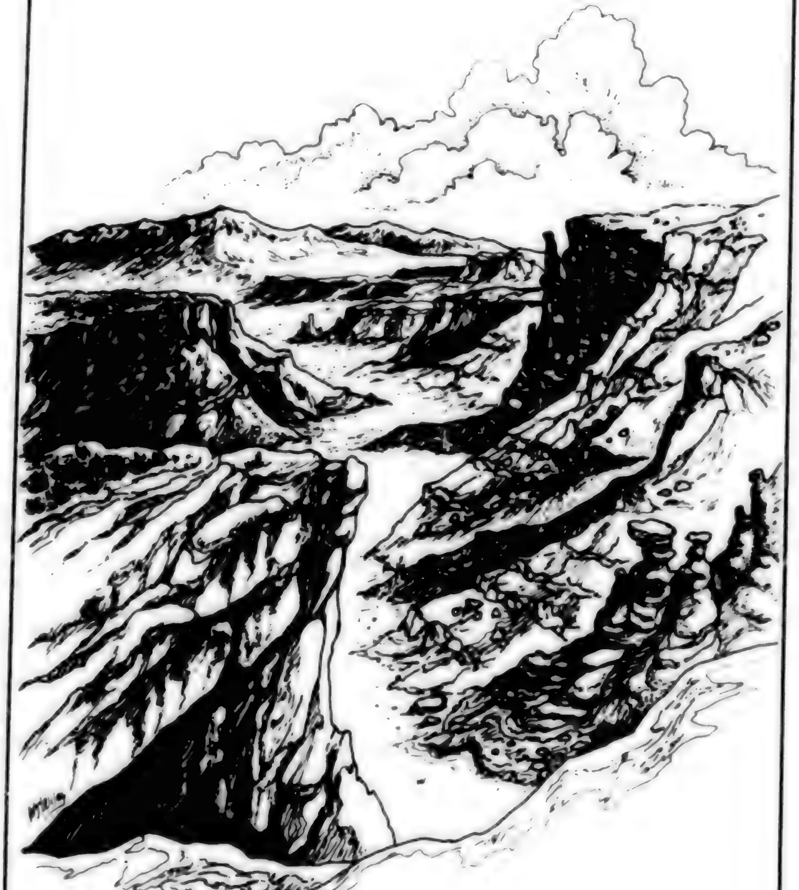
Introduction



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Introduction to the Proceedings of the Third Biennial Conference of Research on the Colorado Plateau

The 16 chapters in this Proceedings were selected from 83 research papers presented at the Third Biennial Conference of Research on the Colorado Plateau. The conference, held in Flagstaff, Arizona on 17–20 October 1995, was hosted by the National Biological Service's Colorado Plateau Research Station (formerly National Park Service Cooperative Park Studies Unit, and now U.S. Geological Survey/Biological Resources Division/Colorado Plateau Field Station), and Northern Arizona University. The theme of this biennial meeting centered around research, inventory, and monitoring on federal, state, and private lands over the Colorado Plateau.

This is the third volume, in a planned series of Colorado Plateau Biennial Conference Proceedings, that highlights research and resource management efforts related to biological, physical, and cultural resources within the biogeographic province of the Colorado Plateau. Many of the papers published in this Proceedings Series have emanated from questions that arose while examining Colorado Plateau resource issues. Because of resource similarities across the Plateau, techniques that work in one management unit are applicable to numerous other management areas. Many protocols, especially those related to monitoring techniques, presently being utilized in lands over the Colorado Plateau stem from aspects of the scientific works published in this Proceedings Series.

Each paper selected for publication represents original research and has been peer-reviewed by a minimum of two reviewers in that particular research discipline. As with the previous two volumes, the papers naturally divide themselves into three major sections: (1) physical resources; (2) cultural resources; and (3) biological resources. However, in this volume the preponderance of contributed papers are from the biological resources arena. Therefore, we start the volume with biological papers, followed by chapters that deal with physical resources, ending with chapters on cultural aspects of the Colorado Plateau.

Biological Resources

It is fitting to begin this section, and book, with a chapter dealing with a unique aspect of the Colorado Plateau -- an endangered native fish, the humpback chub. The R. Valdez chapter is a capstone work that summarizes the many years of research that he has conducted on this endangered species within the 226 miles of the Colorado River from Glen Canyon Dam to Diamond Creek. Valdez and Ryel provide a detailed section on fish distribution patterns among regions of the river. Chub reproduction, coupled with age and growth patterns, provide insight into why this species has become endangered. The authors also provide information on survival, predation rates, and parasite levels within the chub population. The second chapter moves to mammals, with S. Rosenstock providing information on the desert rodent communities of grassland, shrubland, and woodland habitats of Capital Reef National Park. The relatively simple small mammal assemblages that he found parallel the morphology and resource use of small mammals in other North American deserts, suggesting consistent mechanisms that minimize competition and facilitate coexistence. A second mammal chapter, by R. Ockenfels et al., deals with home range size and movement patterns of pronghorn antelope in northeastern Arizona. These authors found that females had larger home ranges than males and that the home range patterns of both sexes were greatly influenced by anthropogenic barriers. The pronghorn freely crossed pasture fences and unfenced roads, but were restricted from crossing fenced roads and fenced railroad rights-of-way. The authors do provide several management alternatives on how to alleviate problems associated with maintaining pronghorn movement across the landscape in Arizona. Chapter 4, by D. Foster et al., is the final mammal study and provides information on distribution of bat species over 5 million acres of forested lands on the southern Colorado Plateau. The authors mist-netted, recorded vocalizations, and utilized an echolocation device at water holes, in an effort to determine the presence and relative abundance of bat species throughout forested regions around Bryce Canyon National Park. The 14 recorded bat species represent sound baseline information for this mammal over portions of the southern Colorado Plateau.

The narrow strips of riparian vegetation, present throughout the southwestern United States, are extremely important to wildlife, and especially so to avian communities. However, these narrow habitat bands provide a challenge to the development of census and monitoring techniques because of the difficulty in identifying techniques that will realistically define changes in avian species numbers and community composition. In Chapter 5, D. Felly and M. Sogge provide a comparison of survey techniques for monitoring birds in riparian vegetation patches along the Colorado River corridor within Grand Canyon National Park. They compare absolute-count with point-count surveys. Their conclusions encourage managers to employ point-count surveys in this habitat, as the authors feel it would be the most effective tool to monitor trends in breeding bird abundances and species composition. The following two chapters also deal with birds, specifically with management questions related to the wild turkey in Arizona. Chapter 6 analyzes the effect of timber harvest on Merriam's turkey loafing habitat. In their analysis of pre- and post-timber harvest sites, B. Wakeling et al. conclude that turkeys need a high canopy density, low horizontal visibility, and contiguous suitable habitat if an area will continue to be used for loafing.

In the next chapter, the same lead author documents winter movement patterns of turkeys as related to their over-night roost sites. Wakeling's findings demonstrate that turkeys concentrate their activities close to roost sites (< 8 km), therefore suggesting that forest manipulation activities should be avoided within .8 km of known roosting areas.

The next five chapters (8–12) of this Proceedings deal with vegetative aspects of Colorado Plateau ecosystems. Haywood et al. assess potential use of the model PROGNOSIS in Arizona forests. The PROGNOSIS model predicts potential suitable wildlife habitat from canopy closure estimate data taken during determination of a stand density index (SDI). The data set developed by the authors, from 230 random vegetation plots over 10,000 ha in the Kaibab Forest, revealed that the PROGNOSIS model explained less than 50% of the variation in the Arizona forest SDI data set. Thus, the authors caution on the use of PROGNOSIS for defining suitable wildlife habitat in Arizona, suggesting that small vegetation sample plots do not provide an accurate indication of forest cover. Chapter 9 documents the status of the rare Goodding willow along the Colorado River in Grand Canyon National Park. Mast and Waring, through tree core sampling, demonstrate the influence of Glen Canyon Dam and flood events on this tree species. The authors also document a recent shift in the distribution of the Goodding willow from the upper to lower canyon regions.

The next two vegetative chapters deal with broad scale analyses of forest stand structure over the southern Colorado Plateau. In Chapter 10, Garrett et al. examine North Kaibab National Forest over-story between 1910 and 1993. They compare analysis from USFS surveys of forest structure from 1910, 1955, 1977 and 1993, showing that smaller and larger classes of trees have increased in density, even with forest product removal. They caution that, with current forest management practices, 25% of the forest is at high risk and 65% at medium risk to catastrophic wildfire or insect/disease loss. Menzel and Covington (Chapter 11), utilizing dendroecological techniques, demonstrate a similar change in the ecotonal *Pinus ponderosa* and *Pinus edulis* forest at Walnut Canyon National Monument, east of Flagstaff, Arizona. They show that subsequent to Euro-American settlement (circa 1876), trees less than 10 cm and those greater than 10 cm diameter at breast height (dbh) have increased in numbers, with the former class going from 72 to 333 stems/ha, while the latter increased from 9.0 to 19.1 m²/ha. In this forest, however, the contribution of *Pinus ponderosa* larger than 10 cm dbh actually decreased (from 80% to 68%) while numbers of *Pinus edulis*, *Quercus gambelii*, and *Juniperus* spp. increased in this tree size class. The authors conclude their chapter with seven management alternatives that might be employed to restore this forest to pre-European conditions.

The final vegetative and biological chapter (12 by T. Graham) describes recovery of a hanging garden from a 1990 fire. Hanging gardens occur over sections of the Colorado Plateau because of unique geologic and hydrologic features. Previous work on this garden in 1983, by Dr. Stanley Welsh of Brigham Young University, provided a baseline of information from which Graham could compare the 5-year recovery of this isolated vegetative community. After monitoring (on an annual basis) soil bacteria, nematodes, and fungi, along with plant species, Graham concluded that recovery for all groups was directly related to soil moisture content. Those areas that did not receive direct moisture from the seeps were still devoid of plants and most microorganisms in 1995, while watered locations have recovered a complete complement of flora and soil fauna.

Physical Resources

The Proceedings now turns to physical aspects of the Colorado Plateau. Chapter 13 by Meretsky and Melis is a transition work that outlines the coordination of biological with physical analyses of data collected during Phase II of the Glen Canyon Environmental Studies (GCES) project. The GCES research effort, directed by Dave Wegner, was a multimillion dollar Bureau of Reclamation project that spanned a period of 12 years, examining the impact on resources along the Colorado River from construction of the Glen Canyon Dam. This chapter summarizes work from Phase II (1989–1993) and how biological and physical information was integrated to produce the 1994 final GCES Environmental Impact Statement. Chapter 14, by Chadwick and Kennedy, describes the depositional environment of Tapeats sandstone in Grand Canyon National Park. From 21 localities, their paleoslope and sedimentological data suggests that this sandstone layer was deposited in deeper waters, not in near-shore environments as was formerly believed. In some instances they argue that sediments were deposited at an excess of 200 m below storm wave base. Further support for their conclusions are provided by the breccia matrix that they examined at 91-mile canyon, which indicates sediment deposition in a reducing environment.

Cultural Resources

Chapter 15 is a brief summary on baseline noise levels and the potential invasion of natural quiet to visitors at Bryce Canyon National Park. To complete this study, Dan Foster established five monitoring locations throughout the park, recording ambient noise levels of jets, helicopters, and fixed-wing aircraft from May to August of 1995. His results establish the types and duration of non-natural noise occurring in the park, providing a baseline that will aid NPS managers in working with future impacts that degrade 'natural quiet' within the region.

The Proceedings closes with an archeological chapter that describes a high altitude agricultural site on the Colorado Plateau. The authors, W. Fawcett and J. Bright, claim that this is one of the highest elevations at which intensive agriculture existed during the first millennium A.D. The water control features that they found, coupled with corn remains at different levels in the excavated cave floor, led the authors to suggest that the inhabitants relied heavily on domesticated cultigens, thus indicating that not all Anasazi were hunter-gatherers during this prehistoric time period.

Acknowledgments

This Proceedings is a direct result of the efforts of numerous agencies and individuals. The dedicated Colorado Plateau Research Station (CPRS) staff provided support in areas of registration (handled by M. Rasmussen, M. Debold, L. Santucci), paper and poster presentations (P. Deshler, M. Sogge, K. Thomas), editorial services (C. Cole), and transportation (C. Drost). Northern Arizona University graduate students (J. Bright, J. Hart, M. Heim, M. Johnson, E. Nowak, D. Willey, H. Yard, J. Zimmerman), led by P. Webster, assisted with logistics at the meeting and operated slide projectors. Thanks are also extended to session chairs and the many reviewers who unselfishly devoted their time and efforts to improving each chapter. Tom O'Shea and Donna O'Leary provided guidance and financial support for this publication.

This book, like the products of other symposia that are centered around a particular problem, should help to focus attention on some of the salient research presently being carried out within the Colorado Plateau. Hopefully, the foundation provided by the research projects published in this Proceedings will help to redirect, and ultimately improve, the quality of research and resource management actions within the Colorado Plateau biogeographic province. Moreover, if this book acts as a stimulus for additional legislative demands and commensurate funding for work on resources of the Colorado Plateau, it will demonstrate that the organizational and editorial efforts of the past 2 years have been well-spent.

CHARLES VAN RIPER III
Colorado Plateau Research Station

Biological Resources

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Life History and Ecology of the Humpback Chub in the Colorado River in Grand Canyon, Arizona

Richard A. Valdez

BIO/WEST, Inc.
1063 West 1400 North
Logan, Utah 84321

Ronald J. Ryel

R. J. Ryel and Associates
1649 North 1000 East
North Logan, Utah 84321

Abstract. The endangered humpback chub (*Gila cypha*) is found as six populations in the Colorado River Basin. The largest is in Grand Canyon, Arizona, where in 1990–1993, fish were distributed as nine aggregations in 307 km of the Colorado River, as well as in the lower 14.9 km of the Little Colorado River (LCR), a seasonally-warmed tributary. An estimated 3,700 adults inhabited the mainstem in 1993, with 3,480 adults in the largest aggregation near the LCR. The LCR was the only area with significant spawning and recruitment of fish to the mainstem, but it was used only by the nearby mainstem aggregation and a resident LCR population. Year-round releases of 8–10°C water from Glen Canyon Dam precluded successful mainstem reproduction and limited growth of young chubs. Adults exhibited a high degree of spatial fidelity for specific river locales; mean net movement was 1.49 km (range = 0–6.11; SD = 1.50) for 69 radio-tagged fish and 1.64 km (range = 0–99.8; SD = 1.72) for 238 Passive Integrated Transponders (PIT)-tagged fish. Annual survival of chubs during the first 3 years of life was estimated at 0.10, while estimated annual survival of adults (age 3+) was 0.93. A major source of subadult mortality was predation by brown trout (*Salmo trutta*) and channel catfish (*Ictalurus punctatus*), which together potentially consumed about 228,850 chubs annually. Adult chubs inhabited primarily large recirculating eddies (88% captures, 74% radio contacts), whereas subadults used shorelines with vegetation, talus, and debris fans, as well as eddy return channels (i.e., backwaters). Diet by volume of mainstem adults near the LCR consisted of *Gammarus lacustris* (freshwater amphipods, 45%), Simuliidae (blackflies, 40%), terrestrial invertebrates (9%), Chironomidae (midges, 5%), and other aquatic invertebrates (1%). Adults from more downstream aggregations consumed a lower proportion of *G. lacustris* and a higher proportion of terrestrial invertebrates. External parasitic copepods (*Lernaea cyprinacea*) were on 8 of 6,294 (<1%) chubs examined and Asian tapeworms (*Bothriocephalus acheilognathi*) were in guts of 6 of 168 (4%) adults flushed with a stomach pump.

Key words: Annual survival, Colorado River, diet, endangered species, *Gila cypha*, Grand Canyon National Park, humpback chub, parasites, predation, reproduction.

The humpback chub (*Gila cypha*) is a large river cyprinid fish that inhabits canyon reaches of the Colorado River Basin (Fig. 1). This indigenous species has declined throughout its range as a result of dam construction, flow modifications, changes in water chemistry, and introduction of competing and predaceous nonnative fishes (Valdez and Clemmer 1982). The humpback chub was included in the first List of Endangered Species on 11 March 1967 (32 FR 4001) and currently remains protected by the Endangered Species Act of 1973, as amended.

Investigations funded by the Bureau of Reclamation, through the Glen Canyon Environmental Studies (GCES) Phase I, 198 -1988, reported that construction of Glen Canyon Dam and subsequent operation jeopardized continued existence of the humpback chub in Grand Canyon through regulated releases of cold hypolimnetic waters (U.S. Department of the Interior 1988). The present study, conducted under GCES Phase II, 1988–1996, was designed to describe physical, chemical, and biological components of the mainstem Colorado River and identify and quantify principal factors limiting the survival of humpback chub in Grand Canyon. The study evaluated life history attributes, including distribution, abundance, movement, reproduction, age and growth, survival, habitat, food habits, predation, and parasites; detailed results were presented in a final project report (Valdez and Ryel 1995). Concurrent, cooperative studies were conducted on the mainstem and tributaries by Arizona Game and Fish Department (1996), Arizona State University (McElroy and Douglas 1995, Douglas and Marsh 1996), and U.S. Fish and Wildlife Service (1994).

Study Area and Methods

The study was conducted in 364 km of the Colorado River in Grand Canyon, Arizona (Fig. 2). Sampling was conducted monthly from October 1990 through November 1993 from Lees Ferry to Diamond Creek. Four study regions were divided longitudinally into 11 geomorphic reaches, previously designated by Schmidt and Graf (1988), and a stratified random design was implemented to sample fish assemblages and associated physical, chemical, and biological components (Valdez and Ryel 1995). Sampling was also partitioned by season for winter (December–February), spring (March–May), summer (June–August), and fall (September–November), and by day, night, dawn, and dusk. Since day length and photoperiod varied with season, a computer program (Sun and Moon Events Worksheet, Heizer Software, Inc.,

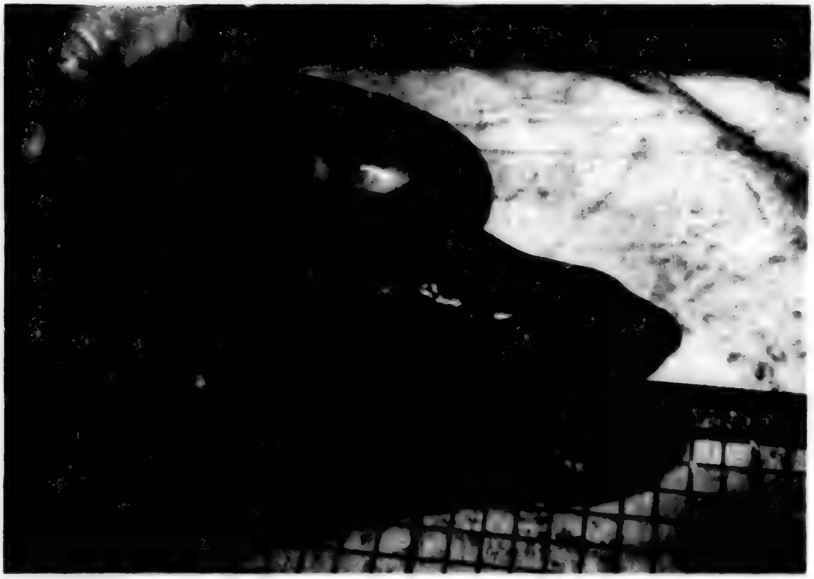

Fig. 1. Adult female humpback chub captured 72 km downstream of Glen Canyon Dam on 15 July 1995. Total length = 480 mm, weight = 1,165 g.

Palo Alto, California) was used to appropriately adjust time blocks. Landmarks in this paper are presented by river kilometer (RK) or distance downstream from Lees Ferry, which is 25.4 km downstream of Glen Canyon Dam.

Fish were sampled with five gear types, including gill and trammel nets, electrofishing, minnow traps, hoop nets, and seines, as described by Valdez et al. (1993). Gill and trammel nets were used to sample large fish in deep habitats; these are standard gears used to survey and monitor other populations of humpback chub in the Upper Colorado River Basin (McAda et al. 1994). Electrofishing was used to sample fish within distinct shoreline types (i.e., vegetation, talus, debris fan, bedrock, cobble bar, sand bar) to evaluate habitat use and reduce variance of catch statistics. Electrofishing was conducted from an Achilles SU-16 research boat with current supplied by a 5000-W generator and routed through a Mark XX Complex Pulse System (CPS) to stainless steel spherical electrodes. Unbaited minnow traps, set in pods of five as replicates, were used to sample the same shoreline types described for electrofishing. Three sizes of winged hoop nets (hoop diameters of 0.6, 0.9, and 1.2 m) were used in shoreline constrictions or at the mouths of backwaters. Two mesh sizes of seines (0.6 and 0.3 cm square mesh) were

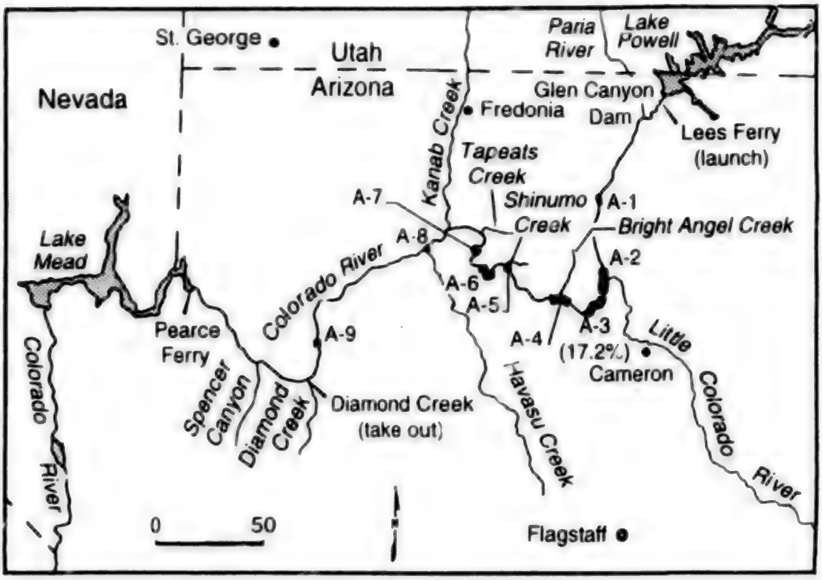

Fig. 2. Study area of the Colorado River in Grand Canyon, Arizona. Nine aggregations of humpback chubs are shown as numbered shaded areas (A-1 to A-9).

used to sample assemblages of small fish in habitats up to about 1.5 m deep. Catch per unit effort (CPUE) was computed for each sample and averaged for stated data partitions.

Humpback chubs were measured for total length (TL), standard length (SL), and forked length (FL) in millimeters, weighed wet in grams, and examined for gender. A nonlethal stomach pump (Wasowicz and Valdez 1994) was used on 168 adults (>250 mm TL) to flush gut contents and evaluate food habits. Scales were taken from chubs smaller than 200 mm TL to determine age and size at which fish moved from the warm Little Colorado River (LCR) to the colder mainstem. Chubs between 60 and 150 mm TL were group-marked with fin-punch combinations, using a 3-mm diameter biopsy needle (Wydoski and Emery 1983), to track longitudinal dispersal of juveniles among subreaches.

Seventy-five adult humpback chubs were surgically equipped with radio transmitters, as described by Tyus (1982), Valdez and Nilson (1982), and Kaeding et al. (1990). Transmitters weighing 9 g (Advanced Telemetry Systems, ATS Model 1 BEI 10-18, battery life of 50 days) were implanted in fish weighing 450–549 g, and transmitters weighing 11 g (ATS Model 2 BEI 10-35, battery life of 75–120 days) were implanted in fish weighing 550 g or more, such that transmitter air weight did not exceed 2% of live fish weight

The transmitters emitted radio signals in the frequency range of 40.600 to 40.740 MHZ at rates of 40, 60, or 80 pulses/min. Movements of these fish were monitored with ATS Model R2000 and Smith-Root Model SR-40 receivers, and were described as net movement (distance between first and last contact points) and gross movement (sum of distances moved between all contact points).

All other fish were measured for TL and SL, weighed, examined for reproductive condition and gender, and released. Selected numbers of brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), channel catfish (*Ictalurus punctatus*), and striped bass (*Morone saxatilis*) were sacrificed and examined for food habits and evidence of predation on native species. All native fishes 150 mm TL or larger were marked with PIT (Passive Integrated Transponders) tags, which were injected into the peritoneal cavity of each fish (Burdick and Hamman 1993).

Results and Discussion

Distribution and Abundance

The first description and photographic documentation of the humpback chub ("bony tail") in the Colorado River in Grand Canyon was by Kolb and Kolb (1914) in 1908 from the LCR near Beamer's Cabin, about 200 m upstream from the outflow (Fig. 3):

> "On the opposite side of the pool the fins and tails of numerous fish could be seen above the water. The striking of their tails had caused the noise we had heard. The 'bony tail' were spawning. We had hooks and lines in our packs, and caught all we cared to use that evening."

The species was described in 1945 by Miller (1946) from three partial specimens believed caught near Bright Angel Creek in Grand Canyon. The earliest catalogued collections of humpback chub and two congeneric species from several locations in Grand Canyon were also by Miller in the 1940s. The 27 specimens are held at the University of Michigan fish collection and include 5 humpback chub, 16 bonytail (*G. elegans*), and 6 roundtail chub (*G. robusta*); these specimens were described morphologically and meristically by Bookstein et al. (1985). Also, Wallis reported eight juvenile humpback chubs from Spencer Creek in 1950 (Kubly 1990). These few historic records show the species was in and near tributary inflows in Grand Canyon, with large numbers reported in the lower LCR, probably during a spawning aggregation. Humpback chubs were also likely in many mainstem areas, based on current distribution and habitat used by upper basin populations (Valdez et al. 1990). Following completion of Glen Canyon Dam in 1963,

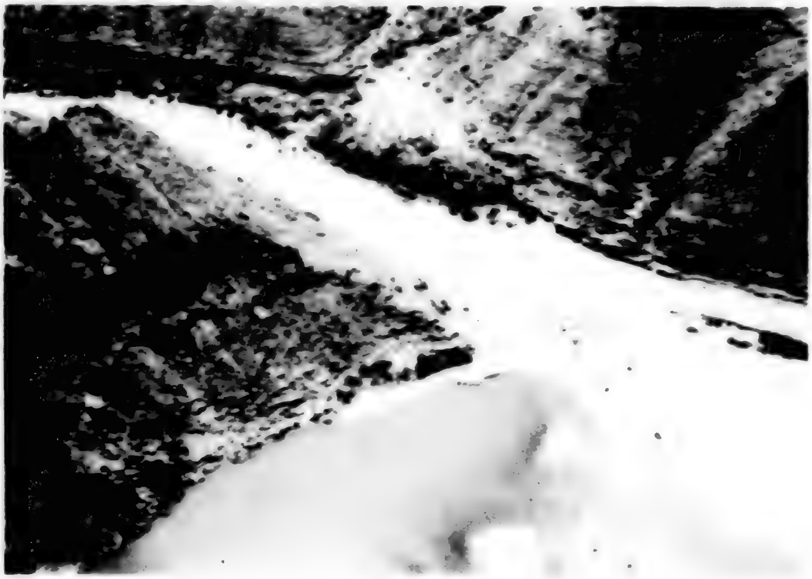

Fig. 3. Aerial view of the Little Colorado River (from upper left) flowing into the Colorado River (left to right) in Grand Canyon, 124 km downstream of Glen Canyon Dam.

humpback chubs were commonly reported in Arizona Game and Fish Department creel census from the Colorado River near Lees Ferry during 1963–1967 (Stone 1964, 1966, Stone and Queenan 1967), but sampling of seven major tributaries (excluding the LCR) between Lees Ferry and Lake Mead in 1968 yielded none (Stone and Rathbun 1968). Holden (1973) collected 15 humpback chubs in July 1967 and 1 in August 1970, all within a few hundred meters downstream of Glen Canyon Dam. Humpback chub have not been captured within 31 km of the dam since 1970 (Carothers and Minckley 1981), which was about the time Lake Powell stratified and cold water releases began to persist year-round (Stanford and Ward 1991). Humpback chubs could have been excluded from the tailwater by these cold releases, by high floods in 1983–1984, or by predation from large rainbow trout weighing up to 7 kg (Carothers and Brown 1991).

From 1970 through 1976, Suttkus and Clemmer (1977) reported young-of-year (YOY) and juvenile humpback chubs between President Harding Rapid (RK 71) and Shinumo Creek (RK 174). Researchers from the Museum of Northern Arizona (Carothers and Minckley 1981) also captured chubs during six river trips in 1977–1979, including adults between North Canyon (RK 31) and Boulder Wash (RK 312), and one juvenile (<100 mm TL) just above Granite Rapid (RK 150). Of 19 tributaries sampled from the Paria River (RK 1.4) to Travertine Creek (RK 369), humpback chubs were captured only in the LCR.

From 1980 through 1981, biologists from FWS captured 504 adult humpback chubs between Nankoweap Canyon (RK 84) and Unkar Rapid (RK 116) (Kaeding and Zimmerman 1983). Fish abundance was reported to resemble a normal or "bell-shaped" distribution with greatest numbers near the LCR inflow. Chubs smaller than 145 mm TL were not caught in the Colorado River above the LCR inflow, although many small specimens were caught in spring and fall below the inflow, providing the first evidence that post-dam chub reproduction was occurring primarily in the LCR. From 1984 through 1989, Arizona Game and Fish Department (Maddux et al. 1987, Kubly 1990) reported humpback chubs in the Colorado River from South Canyon (RK 51) to RK 349, mostly in or near the LCR (RK 99). Ninety-six percent of chubs captured were between RK 51 and RK 140, and specimens were also captured at the inflows of four tributaries, including Bright Angel, Shinumo, Kanab, and Havasu creeks, but not in the tributaries themselves.

The present study, 1990–1993, reported 15 species of fish in the Colorado River between Lees Ferry and Diamond Creek, including 4 native or indigenous species and 11 nonnative or exotic species (Table 1). Humpback chubs were targeted in sampling and were the second most common fish captured with 22% of total catch. The chubs occurred as nine aggregations (Fig. 2; Table 2) in 307 km (from above South Canyon [RK 48] to Granite Springs Canyon [RK 355]), as well as a resident population in the lower 14.9 km of the LCR (Douglas and Marsh 1996). The nine aggregations accounted for 94% of all humpback chubs captured in the mainstem (5,940 of 6,294), or 92% of YOY (2,640 of 2,865), 94% of juveniles (1,545 of 1,638), and 98% of adults (1,755 of 1,791). Total numbers of adults in these aggregations ranged from 5 to 3,482 for a total of about 3,700, based on population estimates in 1993 (Valdez and Ryel 1995). Adults in these aggregations had a high recapture rate, indicating long-term residence and no significant exchange of individuals among aggregations. In a separate study (Valdez et al. 1994), one adult female humpback chub was caught on 5 October 1993 near Maxon Canyon (RK 407) about 44 km downstream of Diamond Creek.

The present distribution of humpback chubs in Grand Canyon shows fish near seasonally-warmed tributary inflows, warm springs, and in reaches with a high frequency of large recirculating eddies formed by debris fans. Historic and recent records, as well as recent life history information, indicate the distribution and abundance of humpback chubs in the Colorado River in Grand Canyon have been reduced. This reduction probably began before Glen Canyon Dam in 1963, as a result of regional land use practices, degraded water quality, and introduction of nonnative fishes (Miller 1961). We estimate 30% loss in distribution of humpback chubs in 364 km of the Colorado River included in this study, primarily as a result of cold dam releases, which limit

Table 1. Fish species captured in the Colorado River from Lees Ferry to Diamond Creek, October 1990 to November 1993.

Common and scientific name	Species code	Status[a]	Young-of-year	Juvenile	Adult	Total	Percent
Family: Cyprinidae (minnows)							
Common carp (*Cyprinus carpio*)	CP	EX	4	44	2,375	2,423	8.6
Humpback chub (*Gila cypha*)	HB	EN	2,865	1,638	1,791	6,294	22.3
Fathead minnow (*Pimephales promelas*)	FH	NN	44	12	1,074	1,130	4.0
Speckled dace (*Rhinichthys osculus*)	SD	NA	4	92	1,395	1,491	5.3
Family: Catostomidae (suckers)							
Bluehead sucker (*Catostomus discobolus*)	BH	NA	101	250	689	1,040	3.7
Flannelmouth sucker (*Catostomus latipinnis*)	FM	EN	183	395	2,197	2,775	9.8
Flannelmouth x Razorback sucker	FR	-	0	0	5	5	<0.1
Unidentified sucker	SU	-	32	0	0	32	0.1
Family: Ictaluridae (catfishes, bullheads)							
Black bullhead (*Ameiurus melas*)	BB	NN	0	3	3	6	<0.1
Channel catfish (*Ictalurus punctatus*)	CC	NN	4	5	104	113	0.4
Family: Salmonidae (trout)							
Rainbow trout (*Oncorhynchus mykiss*)	RB	NN	169	1,152	9,800	11,121	39.4
Brown trout (*Salmo trutta*)	BR	EX	2	107	1,564	1,673	5.9
Brook trout (*Salvelinus fontinalis*)	BK	NN	0	0	6	6	<0.1

Table 1. *Concluded*.

Common and scientific name	Species code	Status[a]	Young-of-year	Juvenile	Adult	Total	Percent
Family: Cyprinodontidae (killifishes)							
Plains killifish (*Fundulus zebrinus*)	PK[b]	NN	1	0	75	76	0.3
Family: Percichthyidae (temperate basses)							
Striped bass (*Morone saxatilis*)	SB	NN	0	0	39	39	0.1
Family: Centrarchidae (sunfish)							
Green sunfish (*Lepomis cyanellus*)	GS	NN	1	1	1	3	<0.1
Family: Percidae (perches)							
Walleye (*Stizostedion vitreum*)	WE	NN	0	0	1	1	<0.1
Totals			3,410	3,699	21,119	28,228	100

[a] NA = native to the drainage
EN = endemic to the drainage
EX = exotic, introduced from another continent
NN = non-native, introduced from another drainage in North America

[b] Common synonym Rio Grande killifish

Table 2. Location and numbers of humpback chub in nine aggregations, 1990–1993.

Aggregations		Location (RK)	Number captured			Estimated number of adults[a]
			Young-of-year	Juvenile	Adult	
A-1.	30-Mile	48–50	14	0	26	52
A-2.	LCR Inflow	92–105	1,830	1,293	1,524	3,482
A-3.	Lava to Hance	106–123	778	226	15	ne
A-4.	Bright Angel Inflow	135–148	13	2	9	ne
A-5.	Shinumo Inflow	174–175	4	13	27	57
A-6.	Stephen Aisle	185–193	0	7	7	ne
A-7.	Middle Granite Gorge	203–208	1	4	124	98
A-8.	Havasu Inflow	251–252	0	0	7	13
A-9.	Pumpkin Spring	342–343	0	0	6	5
Total			2,640	1,545	1,755	3,707

[a] Based on population estimates by Ryel and Valdez (1996).

[b] ne = no estimate because of insufficient recaptures.

reproduction, reduce food supplies, and maintain populations of large coldwater predators (i.e., trout). We also conclude an inferred reduction in abundance of chubs because of limited mainstem reproduction and survival, but the absence of historic estimates precludes assessing the magnitude of reduction. Assimilation of literature on humpback chub (Minckley 1996) reveals collections after about 1980 indicate distribution of the species has not changed dramatically in the last 13 years. Density estimates for the mainstem are not available to quantify changes in abundance, although Douglas and Marsh (1996) showed a decrease in adults in the LCR over the last decade.

Movement

Radio-tagged adult humpback chubs (>350 mm TL) moved relatively little during this study, suggesting strong fidelity to specific mainstem locales. Of 69 fish tracked for an average of 93 days (range = 30–170) near the mouth of the LCR (RK 92-105), mean net movement (Fig. 4a) was 1.49 km (range = 0.00–6.11; SD = 1.50), while mean gross movement was 5.13 km (range = 0.32–16.93; SD = 3.27). Spawning-related movements into and from the LCR were not included in this analysis. PIT-tagged chubs (≥150 mm TL) exhibited similar average net movement (Fig. 4b) of 1.64 km (range = 0.0–99.8; SD = 1.72) for consecutive captures separated by 1 to 1,065 days (238 fish, 285 movements). Movements of PIT-tagged fish were equally divided between upstream and downstream directions, with 85% of net movements less than 2 km. Net movements were not significantly different (t = 1.66, P = 0.098, df = 192) between males (n = 102; mean = 0.89 km; range = 0.0–4.9) and females (n = 92; mean = 1.22 km; range = 0.0–8.9), or between 238 PIT-tagged fish and 69 radio-tagged fish (t = 0.17, P = 0.867, df = 352). Movement of humpback chubs in Grand Canyon was similar to that reported for the species in Black Rocks, Colorado River, Colorado, where mean net movement was 0.8 km (range = 0–3.7) for 8 radio-tagged adults and 1.6 km (range = 0–23.0) for 16 Carlin-tagged adults (Valdez and Clemmer 1982). Kaeding et al. (1990) reported mean displacement for 30 radio-tagged adults of 0.8 km (range = 0–8.4; SD = 0.4) for the same area.

Although movement in the Colorado River in Grand Canyon was similar to that in Black Rocks, annual spawning-related movements of 419 PIT-tagged adults between the Colorado River and LCR resulted in a higher mean net movement of 6.4 km (range = 0.10–20.0; SD = 5.9), with means of 2.0 km (range = 0.0–6.5; SD = 1.6) in the mainstem and 4.4 km (range = 0.0–14.9; SD = 3.8) in the LCR. These fish were recaptured up to 14.9 km up the LCR, with 44% more than 3 km and 36% more than 5 km from the mouth (Fig. 5). Mean net movement was not significantly different between males (6.5 km) and females (5.8 km) (n = 372; t = 1.41; P = 0.075 df = 370). Net movements of PIT-tagged fish captured by Arizona State University in the LCR and recaptured by us in the mainstem were similar.

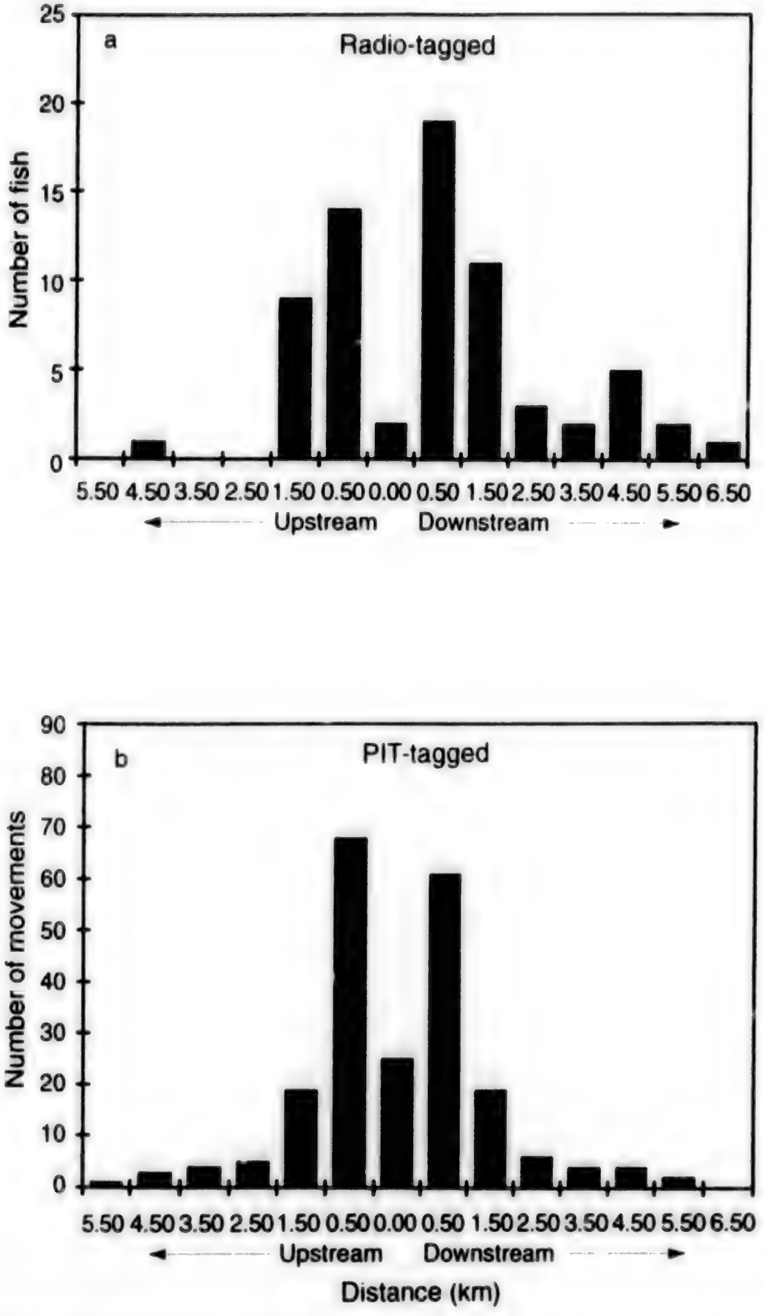

Fig. 4. Net movements of 69 radio-tagged adult humpback chubs (a) and 238 PIT-tagged adults (285 movements) (b) in the Colorado River, October 1990 through November 1993.

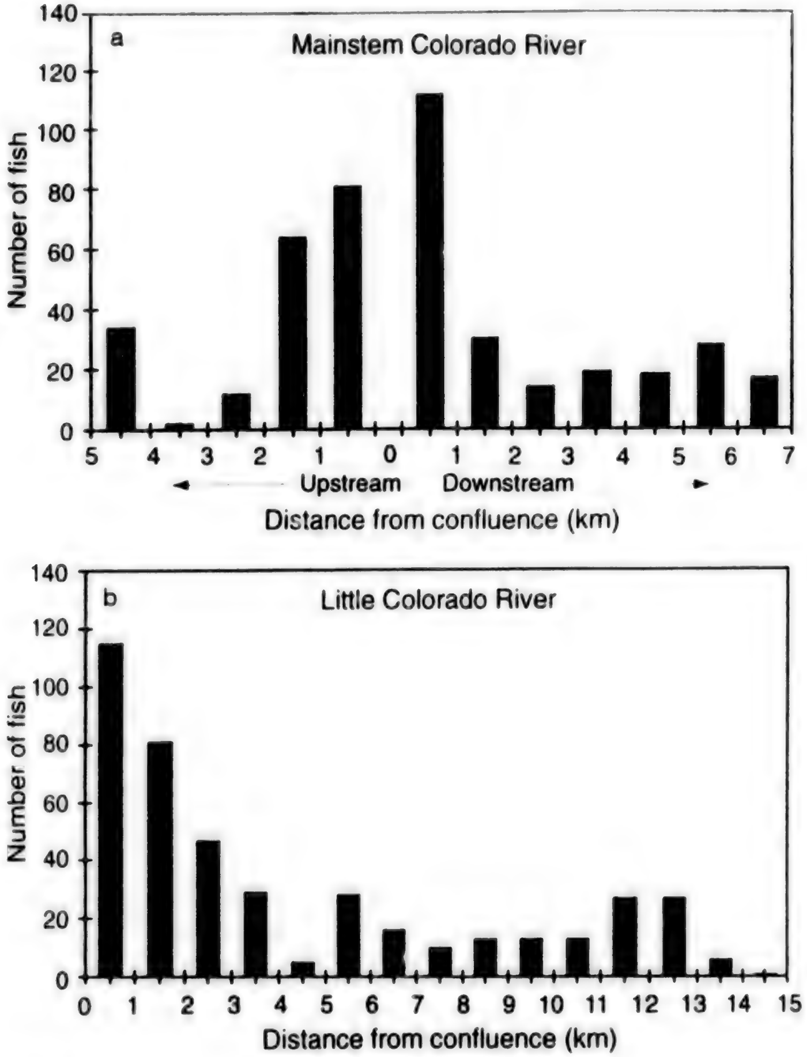

Fig. 5. Capture locations in the mainstem Colorado River (a) and recapture locations in the Little Colorado River (LCR) (b) for 419 PIT-tagged adult humpback chubs, October 1990 through November 1993. LCR recapture courtesy of M. E. Douglas and P. C. Marsh, Arizona State University.

Fish captured between RK 0 and RK 14.9 in the LCR were recaptured in the mainstem up to 4.9 km upstream and 24.2 km downstream of the LCR confluence (RK 94-123). Mean net movement of 401 fish (415 movements) from the LCR to the mainstem was 7.2 km (range = 0.08–34.10; SD = 6.8), with means of 5.3 km (range = 0.0–14.9; SD = 4.9) in the LCR and 1.9 km (range = 0.0–24.2; SD = 2.1) in the mainstem. Mean net movement from the

LCR to the mainstem was not significantly different between males (7.4 km) and females (7.2 km) ($t = 0.30$, $P = 0.76$, df = 357). Neither net movements nor timing of movements differed between males and females, indicating both sexes moved simultaneously into the LCR for spawning.

More than 99% of PIT-tagged fish captured in the mainstem and the LCR remained within a 13-km subreach of the mainstem (i.e., 6.5 km upstream to 6.5 km downstream of the LCR confluence) and a 14.9-km reach of the LCR (confluence to Chute Falls), indicating maximum home range of individuals in this population was about 28 km. The greatest cumulative movement for a PIT-tagged fish was entirely within the defined home range, i.e., 54.9 km for an adult recaptured six times in 626 days, twice moving between RK 10.0 in the LCR and RK 93.8 in the mainstem. Both movements were during spawning periods, and in both cases the fish returned to original mainstem locations. Movement from the mainstem to a tributary for spawning is unique for this species. Valdez and Clemmer (1982) and Kaeding et al. (1990) found little movement during spawning in Black Rocks, and determined that suitable habitat for all life history needs was found within the confined 5-km reach occupied by that population. Similar findings are reported for other populations, including Westwater Canyon (Utah Division of Wildlife Resources [UDWR] 1994a) and Desolation Canyon, Utah (UDWR 1994b), Cataract Canyon, Utah (Valdez 1990), and Yampa Canyon, Colorado (Karp and Tyus 1990).

Fidelity of PIT-tagged chubs to specific locales or reaches in the mainstem was consistent following spawning movements. Of 73 PIT-tagged fish consecutively captured in the mainstem, LCR, and again in the mainstem (round trip movements), 59 (81%) returned to within 2 km of specific mainstem locales and 38 (64%) were within 1 km. Movement among the nine aggregations was rare; only 7 of 238 (2.9%) PIT-tagged fish recaptured in the mainstem moved to other aggregations.

Reproduction

Overall male to female ratio of humpback chub in Grand Canyon was 49:51. Most successful spawning during this study occurred in the LCR by mainstem fish from the vicinity of the LCR, as well as by LCR residents. Successful mainstem spawning was precluded by cold dam releases, although evidence of reproduction (i.e., YOY) was found in warm shoreline springs about 48 km upstream of the LCR. Kaeding and Zimmerman (1983) found that, despite nearly constant mainstem temperatures, peak gonadal maturation of fish near the LCR inflow occurred in spring. We found that, of 178 adult chubs from the mainstem near the LCR during 1990–1993, peak spawning characteristics (i.e., expression of milt or eggs, tubercles, coloration) occurred in March, while 48 mainstem adults from other aggregations peaked in May, nearly 2 months later. These mainstem adults were from Middle Granite Gorge (RK 204–217; $n = 23$), near South Canyon (RK 48; $n = 7$), and inflows of Clear Creek (RK 135; *n* = 4), Bright Angel Creek (RK 141; *n* = 1), Shinumo Creek (RK 175; *n* = 5), and Havasu Creek (RK 252; *n* = 5). Ripe fish were captured in the mainstem from March through July at maximum water temperatures of 10–14°C, a range marginal for survival of eggs and larvae of humpback chub (Hamman 1982). Hatching success under laboratory conditions was 12%, 62%, 84%, and 79% at 12–13°C, 16–17°C, 19–20°C, and 21–22°C, respectively, while survival of larvae was 15%, 91%, 95%, and 99%, respectively (Hamman 1982). Marsh (1985) found similar relationships of temperature and survival. Despite the presence of ripe fish near tributaries, eggs and larvae were not found in inflows. Past investigators reported spawning by humpback chubs in the LCR in March, April, and May at water temperatures of 16–20°C (Suttkus and Clemmer 1977, Carothers and Minckley 1981, Kaeding and Zimmerman 1983).

These results suggest mainstem fish away from the seasonally-warmed LCR continue to achieve reproductive condition at about the same time as other populations in the basin (Valdez and Clemmer 1982), despite relatively constant river temperatures. Chubs in spawning condition were reported in Cataract Canyon, Utah at water temperatures of 16°C in June 1988 (Valdez and Williams 1993), and in Black Rocks at 11.5°C in June 1980 (Valdez and Clemmer 1982) and at 13–17°C in June 1983 and 15–23°C in July 1984 (Kaeding et al. 1990).

Although we found no evidence of spawning by humpback chubs in tributary inflows, reproduction was associated with a warm shoreline spring near RK 48. On 12 July 1994, about 100 YOY chubs were sighted among boulders in the warm plume and 14 voucher specimens (18–31 mm TL) were collected. Water temperature at the spring source was constant at 21.5°C, compared to 11°C in the adjacent mainstem. We believe these young fish hatched from eggs deposited in the warm spring plume, since mainstem water temperatures were too cold for survival of eggs or larvae (Hamman 1982, Marsh 1985). Based on average length of 24 mm TL (20 mm SL), these young were hatched about 8 June 1994 and were approximately 36 days old (D), as determined by the relationship $D = (\ln SL - \ln 7.2843) / 0.0280$ (Muth 1990). An estimated 50 adults inhabit a warm spring complex near RK 48; these fish are about 50 km upstream of the LCR and are likely remnants of a mainstem population that inhabited Grand Canyon prior to Glen Canyon Dam.

Evidence of successful reproduction in this area was also reported by Arizona Game and Fish Department (1994); 20 YOY (20–50 mm TL) chubs were collected from a backwater near President Harding Rapid (RK 71) in 1993. These and other juveniles reported from this area (Suttkus and Clemmer 1977, Carothers and Minckley 1981) likely hatched from eggs deposited in these warm springs, since other warm suitable spawning habitats have not been identified in the area. Furthermore, these fish were 32–48 km upstream of the only known spawning area, the LCR, and it is unlikely these young fish could swim this distance upstream.

Age and Growth

Average lengths of mainstem subadults at 1, 2, and 3 years, based on back-calculations from scale annuli, were 96, 144, and 186 mm TL, respectively. The majority of growth in the first year occurred in the LCR, since scale checks, indicating disrupted growth when the fish moved from the warm LCR to the colder mainstem, showed fish averaged 74 mm TL at time of descent; minimum size was 52 mm TL, indicating little or no survival of smaller fish descending from the LCR. The most likely cause of mortality was thermal shock or predation illicited by aberrant thermal-shock behavior, i.e., erratic swimming and flashing. Although no previous growth data were available for mainstem chubs, Kaeding and Zimmerman (1983) reported first scale annulus formation at 100 mm TL for LCR fish and 3-year-old fish were 250–300 mm TL.

Average length of females (*n* = 599) was 355 mm TL (range = 200–480) and average length of males (*n* = 623) was 338 mm TL (range = 202–460). Average weight of females was 454 g (range = 85–1,165) and average weight of males was 375 g (range = 43–1,122). These field observations indicate both males and females in Grand Canyon mature at about 200 mm TL or 3 years of age.

A logarithmic relationship (Von Bertalanffy 1938, Ricker 1975) was used to describe growth of chubs in the mainstem and LCR (Fig. 6). Mainstem growth rates were based on scale back-calculations for ages 0–3 and recaptured PIT-tagged fish for ages 4+. Assuming a length of 7 mm at hatching (Muth 1990), annual growth increments for 1, 2, and 3 years were 89 mm (7 to 96 mm TL), 48 mm (96 to 144 mm TL), and 42 mm (144 to 186 mm TL), respectively. Average 30-day growth rates were 10.3 mm (7 to 74 mm TL) for fish in the LCR, and 4.0 and 3.5 mm for 2 and 3-year olds, respectively, in the colder mainstem. Lupher and Clarkson (1994) reported average 30-day growth of laboratory chubs of about 2.3 mm at 10°C and about 10.6 mm at 20°C. The 30-day growth rate of 10.6 mm is comparable to 10.3 mm determined for the LCR fish from this study, but the higher rates of 4.0 and 3.5 mm for mainstem fish (compared to 2.3 mm) may be attributed to wild fish spending time in warm shallow shorelines or backwaters.

Average 30-day growth rates of recaptured PIT-tagged fish by 50-mm increments in the mainstem were 2.3 mm (150–200 mm TL), 2.8 mm (200–250 mm TL), 2.5 mm (250–300 mm TL), 1.2 mm (300–350 mm TL), 0.8 mm (350–400 mm TL), and 0.9 mm (>400 mm TL). Average growth rate of PIT-tagged fish in the mainstem was 16.6 mm per year. By comparison, average 30-day growth rates of chubs from the LCR (Minckley 1992) were 1.4 mm (<200 mm TL), 1.3 mm (200–250 mm TL), 1.1 mm (250–300 mm TL), 0.4 mm (300–350 mm), 0.5 mm (350–400 mm), and 0.1 mm (>400 mm TL). Average growth for all sizes and ages of LCR fish handled by Minckley was 13.5 mm per year. These results show growth rates of juveniles are higher

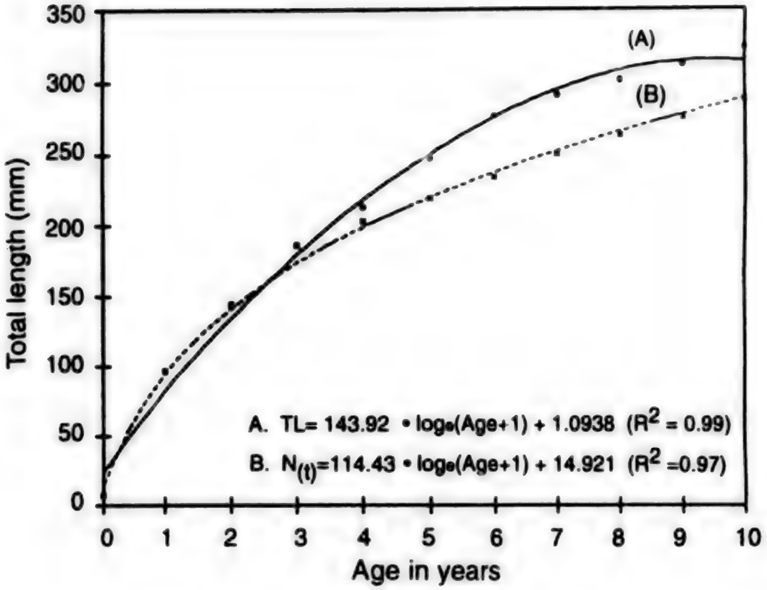

Fig. 6. Logarithmic growth curve for humpback chubs in the mainstem Colorado River (A) and in the Little Colorado River (B). Hatching length of 7 mm (Muth 1990) assumed. Length at 1–3 years from scale back-calculations; lengths at 50 mm increments for 4+ years from PIT tag recaptures. Growth curve for humpback chub in the LCR from Minckley (1992).

in the seasonally-warmed LCR than in the mainstem, but higher for adults in the mainstem. This difference may be related to differential food availability between rivers and limited space in the LCR for adults (Valdez and Ryel 1995).

Survival

Mean monthly electrofishing catch rates (CPUE) for subadult humpback chubs (<200 mm TL) along mainstem shorelines (excluding backwaters) from the LCR to Hance Rapid in 1991, 1992, and 1993 peaked at 16.0, 15.5, and 52.2 fish/h, respectively. Successive decreases in densities are described as negative exponentials (Z_t; Ricker 1975), which showed similar semiannual survival rates of 0.31 and 0.33 for 1991 and 1992, respectively, but only $1x10^{-4}$ for 1993 (Fig. 7). Estimated annual survival rates were 0.10, 0.11, and

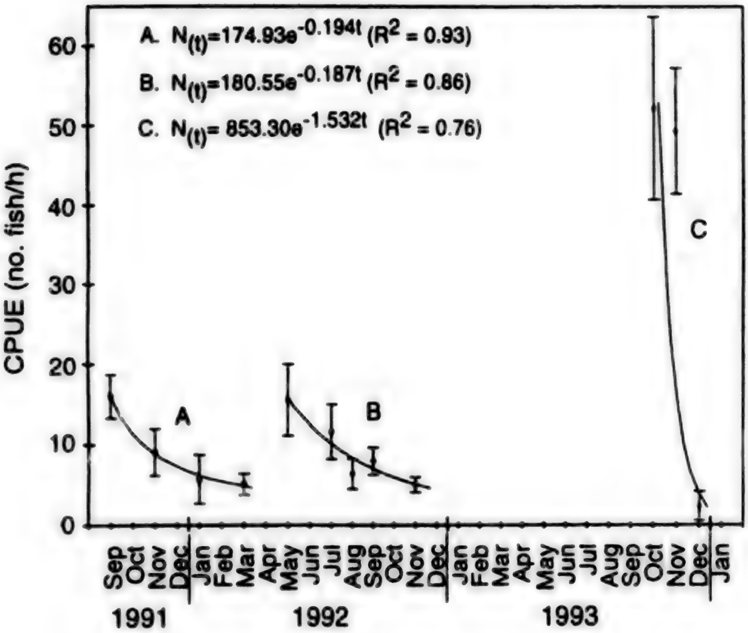

Fig. 7. Exponential decreases in densities of subadult humpback chubs in the Colorado River from the Little River confluence (RK 99) to Lava Canyon (RK 105) for September 1991 through March 1992 (A), May through November 1992 (B), and September through November 1993 (C).

1×10^{-8}, respectively. The average annual survival rate of adults during 1991–1993, using Jolly-Seber model estimators (Brownie et al. 1985), was 0.93 (95% CI = 0.89–0.97).

The main source of young chubs to the mainstem during our study was the LCR, with peak numbers descending during monsoon-induced freshets from May through September. Densities and distributions of subadults downstream of the LCR indicate some young fish dispersed to downstream aggregations. However, based on survival rates of subadults between the LCR and Hance Rapid and small numbers of subadults in other downstream aggregations, survival of young in the mainstem was low. Possible causes of mortality were identified as predation, starvation, and thermal shock.

Habitat

Most subadult chubs in the mainstem were along shorelines and most adults were offshore. An apparent transition in habitat use occurred with size and age, such that subadults moved from shoreline to offshore habitats beginning at about 1 year of age and ending at about 3 years of age, when fish reached maturity at 180–200 mm TL. Electrofishing CPUE of subadults was significantly higher (ANOVA, $P = 0.05$) in shorelines with vegetation (3.0 fish/h), talus (1.7 fish/h), and debris fans (0.9 fish/h) than those with bedrock, cobble, and sand (<0.5 fish/h) (Fig. 8).

The majority of adults in the mainstem were in large recirculating eddies (88% of adults captured and 74% of radio contacts), which comprised about 21% of surface area in the 13.5-km subreach sampled near the LCR inflow. Smaller percentages of adults were captured or radio-contacted in runs (7% and 16%, respectively) that comprised an average of 56% of surface area. Conversely, return channels, which were less than 1% of surface area, accounted for 4% of captured adults and 7% of radio contacts. Small numbers of adults (<1%) were also captured or contacted in pools and riffles, and although fish were neither caught nor radio-contacted in rapids, movement patterns indicate chubs ascended and descended rapids with drops of 1–3 m. Selection of eddy complexes may be related to use of low velocity habitat and greater food availability from entrainment of suspended material (Fig. 9). Relatively small movements in all seasons are attributed to proximity of feeding, resting, and cover habitats within small reaches of river. We found a consistent relationship between frequency and occurrence of debris fans, which form eddy complexes, and occurrence and numbers of adult humpback chub in Grand Canyon.

Food Habits

Gut contents of 168 adult chubs were collected with a stomach pump during 1991–1993. Of these, 10 (5.9%) had empty guts and were not included in the analyses. Of the remaining 158 fish, Simuliidae (blackflies), Chironomidae (midges), and *Gammarus lacustris* (freshwater amphipods) were in 78%, 58%, and 51% of guts, respectively. Other aquatic invertebrates, including Cladocera (water fleas), Neuroptera (spongillaflies), and Trichoptera (caddisflies) were found in 20%, 6%, and 5%, of guts, respectively. The most common terrestrial invertebrates were Hymenoptera (primarily ants), Coleoptera (beetles), and Diptera (true flies), which were in 21%, 15%, and 11% of guts, respectively. Hemiptera (true bugs), Orthoptera (grasshopper, crickets), and Homoptera (cicadas) were in 3%, 2%, and 2% of guts, respectively.

The composite volumetric diet of adults sampled near the LCR ($n = 128$) (excluding the green algae *Cladophora glomerata*) consisted of *G. lacustris* (45%), Simuliidae (40%), terrestrial invertebrates (9%), Chironomidae (5%),

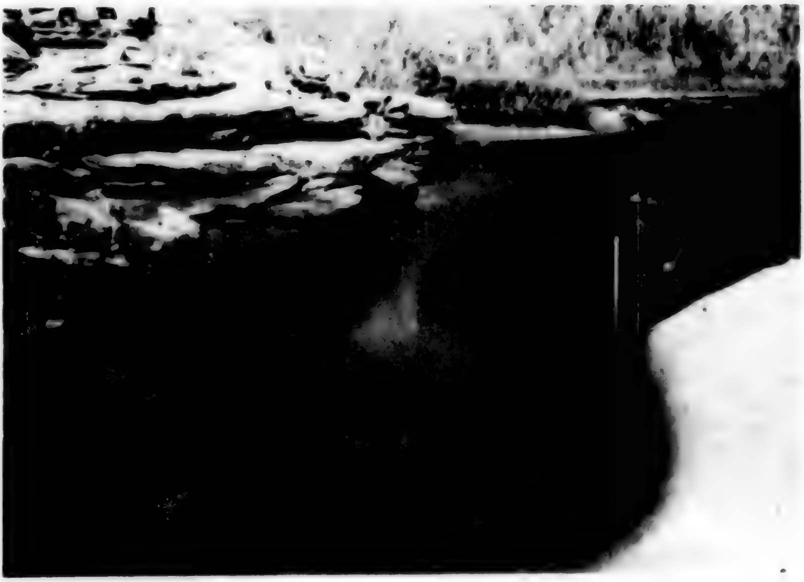

Fig. 8. Talus shorelines (top) and eddy return channels or backwaters (bottom) used by subadult humpback chubs in the Colorado River in Grand Canyon.

Fig. 9. The Colorado River in Grand Canyon about 127 km downstream of Glen Canyon Dam. Large lateral debris fans form recirculating eddies used by adult humpback chubs and associated sand bars.

and other aquatic invertebrates (1%) (Fig. 10); *C. glomerata* was found in 22% of chubs examined and comprised 23% of gut content volume. The diet by volume of adults from a more downstream aggregation in Middle Granite Gorge (MGG, *n* = 24) comprised of Simuliidae (49%), terrestrial invertebrates (30%), *G. lacustris* (10%), Chironomidae (5%), and other aquatic invertebrates (6%); *C. glomerata* was not present in guts of these fish. The high incidence of Simuliidae in gut contents was consistent between the LCR and MGG aggregations. Notable differences in diet between the two aggregations included a higher incidence of *G. lacustris* and *C. glomerata* in the LCR aggregation and a higher incidence of terrestrial invertebrates in the MGG aggregation. These results suggest terrestrial invertebrates become increasingly important to chubs in downstream reaches of Grand Canyon where aquatic food supplies are correspondingly lower.

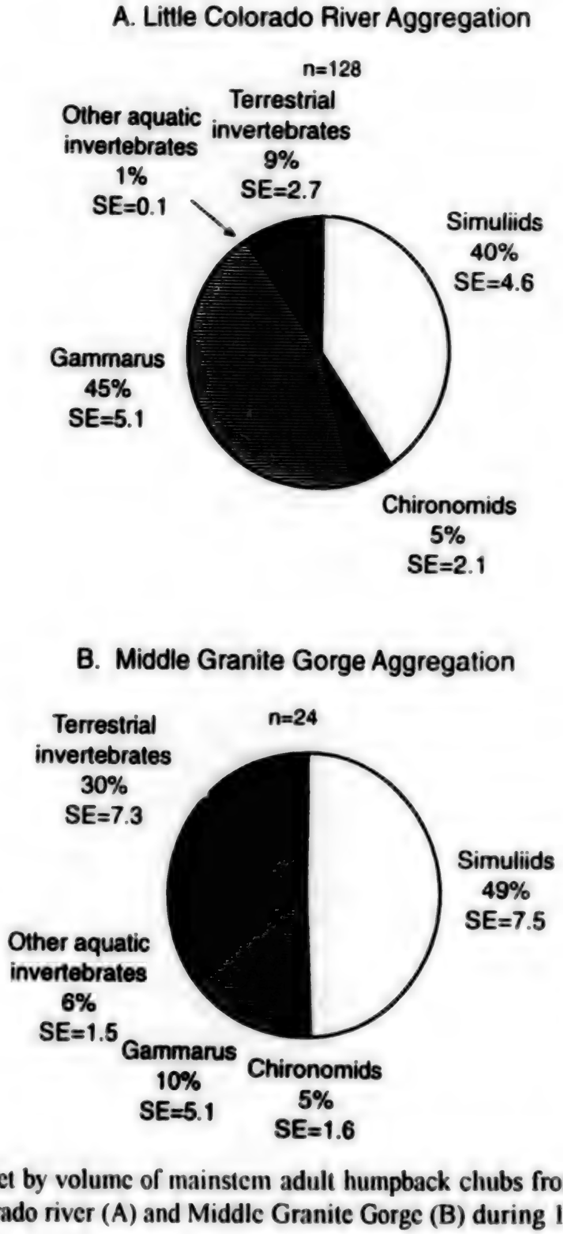

Fig. 10. Diet by volume of mainstem adult humpback chubs from near the Little Colorado river (A) and Middle Granite Gorge (B) during 1992–1993.

Predation

Of 328 stomachs taken from nonnative fishes in Grand Canyon in 1990–1993, only 6% contained fish remains and only two species--brown trout and channel catfish--contained remains of humpback chub. Of 48 brown trout, 9 (19%) contained remains totaling 15 fish, and 5 (10%) contained in total 10 humpback chub; 1 brown trout contained 4 chubs. Brown trout preying on chubs were 393–500 mm TL, and ingested chubs were 78–130 mm SL (mean = 95). Brown trout with ingested chubs were caught between RK 92 and RK 105, above and below the LCR inflow (RK 99).

Five of 68 (7%) channel catfish examined contained remains of 8 fish, including 1 humpback chub (95 mm SL), 1 bluehead sucker (*Catostomus discobolus;* 150 mm SL), 1 flannelmouth sucker (*C. latipinnis*; 170 mm SL), 1 unidentified sucker, and 4 unidentified fish. The catfish with the chub was 475 mm TL, and was captured at RK 99, immediately below the LCR inflow. Predation of humpback chub by channel catfish was also reported in the LCR by Arizona Game and Fish Department (C.O. Minckley, personal communication) and Arizona State University (M. Douglas, personal communication).

These findings indicate a population of 3,000 adult brown trout in Grand Canyon could consume approximately 227,760 subadult chubs annually and a population of 200 adult channel catfish could consume approximately 1,095 subadults annually. One unidentified fish was found in stomach contents of 163 rainbow trout (<1%). The dominance of invertebrates and algae and the absence of fish reflect the typical diet of rainbow trout in Grand Canyon (Maddux et al. 1987, Leibfried 1988). Of 39 striped bass (mean = 453 mm TL, range = 315–857 mm TL) captured in regions II and III, four (10%) contained remains of seven fish, including three trout and four unidentified fish. Striped bass may prey on humpback chub in Grand Canyon, but the magnitude of predation is probably small because of small numbers involved in annual spawning runs from Lake Mead (17 captured in 1991, 3 in 1992, and 19 in 1993) and the likelihood that these fish fast during spawning migrations (Stevens et al. 1987).

Parasites

The only external parasite on humpback chubs from the mainstem was the parasitic copepod, *Lernaea cyprinacea*. Eight of 6,294 (<1%) chubs were infected with an average of 1.25 copepods per fish (range = 1–2). None of the infected fish showed signs of stress or illness, although small open lesions were common at attachment sites. Valdez et al. (1982) reported this parasite on 26% of 234 humpback chubs from the upper Colorado River; it was not on YOY, but 17% of juveniles, and 31% of adults were infected with 1–13 copepods.

We attribute the low incidence of *L. cyprinacea* in Grand Canyon to persistent suboptimal mainstem temperatures. The favorable temperature range for this parasite is 14–32°C; temperatures outside of this range prevent hatching and transformation of female larvae (Shields and Tidd 1968). Although maturation occurs in 15 days at 30°C (Stoskopf 1993), the parasite is unable to complete its life cycle at temperatures below 14°C, pH below 7.0, and salinity at or above 1.8% (Hoffman 1976). Copepods have been observed parasitizing fish only when water temperature exceeds 25°C (Marcogliese 1991); hence, infection by this parasite probably occurs primarily in warmed tributaries and persistently warm habitats, such as long-lived backwaters or marshes.

The only internal parasite observed in chubs during this study was the Asian tapeworm, *Bothriocephalus acheilognathi*, which was in the gut of 6 of 168 (4%) adults flushed with a stomach pump and averaged 6.7 tapeworms (range = 1–28) per infected fish. Because the stomach pumping technique may not be effective at flushing this tapeworm from the gut of fish, this reported frequency and intensity of infestation may be an underestimate. Subadult chubs were not examined internally or subjected to stomach flushing.

Asian tapeworms were first reported in humpback chubs from Grand Canyon in 1990 (D. Hendrickson, personal communication). Angradi et al. (1992) reported this parasite in 80% of juveniles (range = 13–35 mm TL) from the LCR in 1990, but none in 1989. Asian tapeworms were first reported in North America in 1975 in golden shiners (*Notemigonus crysoleucas*) and fathead minnows (*Pimephales promelas*) and in the United States in grass carp (*Ctenopharyngodon idella*) (Hoffman 1976). The primary host is one of several species of cyclopoid copepods, and the principal adult hosts are members of the minnow family, although it has also been found in non-cyprinids in Asia and Europe (Babaev 1965, Bauer et al. 1969), where it is considered a dangerous fish parasite. Asian tapeworms can grow to 100 mm long and 2 mm wide with a large triangular scolex or head, which is characteristic for the species.

Temperature has a significant effect on maturation and growth of *B. acheilognathi* (Granath and Esch 1983). Maximum egg hatching and development of all life stages occurs at 30°C, although stimulation for growth, development, and maturation of eggs occurred above 25°C. Highest densities of tapeworms were found at 20°C (temperatures below 20°C were not tested). Thus, while this parasite can live in fish at mainstem temperatures, full development and infection of other fishes can occur only in persistent warm habitats with appropriate primary hosts.

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Desert Rodent Communities of the Canyon Country Province, Colorado Plateau

Steven S. Rosenstock[1]

Wingate Eco-Logic
P.O. Box 462
Fredonia, Arizona 86022

Abstract. From 1988–1991, I studied desert rodent communities of the Canyon Country Province, Colorado Plateau. Study areas were located in Capitol Reef National Park, Utah and represented grassland, shrubland, and woodland habitats. I examined species richness, guild structure, body size, and microhabitat use, testing predictions based on patterns documented in other North American desert rodent faunas. Rodent assemblages were relatively simple with respect to species richness and number of taxonomic/foraging guilds. Among coexisting species, only the numerically dominant omnivores exhibited non-random body size. Co-occurrences of species representing three taxonomic-foraging guilds were significantly different from expected and, in one case, correlated with microhabitat use. Desert rodents of the Canyon Country have evolved patterns of morphology and resource use similar to those documented in other North American deserts that may minimize competition and facilitate coexistence.

Key words: Body size, community structure, desert rodents, microhabitat.

Desert rodent communities have received considerable attention from ecologists because of their relative simplicity and ease of study. Research conducted in North American deserts has greatly expanded understanding of small mammal community structure, particularly patterns of species richness, morphology, and resource use. Most previous studies have been conducted in the Great Basin, Mojave, and Sonoran deserts and have largely focused on members of the family Heteromyidae (kangaroo rats and pocket mice). Consequently, prevailing views of desert rodent community structure have a distinct taxonomic and regional bias (Reichman 1991). In contrast, small mammal communities of the Colorado Plateau have received much less attention. It is unknown to what degree they share structural patterns documented in more well-studied arid ecosystems. Variability in species richness is a fundamental attribute of desert rodent assemblages, a consequence of historical and ongoing evolutionary, biogeographic, ecological, and population processes (Brown and Kurzius 1989, Brown and Zeng 1989, Whitford and Steinberger 1989, Brown and Heske 1990). Brown and Kurzius (1987) examined desert rodent species richness at regional scales, synthesizing results of studies conducted across the western United States, but largely excluding the Colorado Plateau. They reported three underlying patterns: (1) a large number of species combinations, most of which occurred only a few times; (2) species richness lower than expected if species combinations were random; and (3) greater than expected occurrence of assemblages containing relatively few species. Similar results have also been found at microspatial (plot and trapsite) scale (Brown and Kurzius 1989).

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[1] Arizona Game and Fish Department, Research Branch, 2221 West Greenway Road, Phoenix, Arizona 85023.

The Canyon Country Province of the Colorado Plateau is characterized by tremendous topographic and vegetative diversity, and a high degree of habitat interspersion. Consequently, a large number of desert rodent assemblages can be found within a relatively small geographic area (Rosenstock 1992). This represents a unique opportunity to test patterns of species richness and co-occurrence in an area that has received little previous attention and at a scale intermediate to that considered in previous studies.

Differences in body size among coexisting, potentially competing species are a common structural characteristic of North American desert rodent faunas (Brown 1987). Coexisting species tend to exceed critical ratios of body mass, often termed Hutchinson's ratios. This pattern is most evident (and well-studied) among granivorous Heteromyids (Bowers and Brown 1982). Body size relationships among other taxa have received much less attention. Canyon Country rodent communities are often dominated by omnivorous Cricetids and Sciurids. Coexisting species in this ecoregion might also exhibit non-random patterns in body size, differences that should be most apparent among species using similar resources.

Because members of a given guild (sensu Root 1967) use similar resources, the potential for competition is high. Brown (1987:193) proposed that coexisting desert rodents tend to belong to different taxonomic and functional groups. However, members of the same guild that coexist must partition available resources. Such partitioning is often reflected in microhabitat use. Among sympatric granivorous Heteromyids, there is strong evidence of microhabitat segregation (Kotler 1984, Price and Heinz 1984, Price and Waser 1985, Reichman 1991). However, understanding of such relationships among other desert rodents is limited. Coexisting rodents of the Canyon Country Province might also be expected to show similar separation.

Hypotheses

I examined patterns of species richness, body size, guild structure, and microhabitat use in desert rodent assemblages of the Canyon Country Province, Colorado Plateau. I tested four sets of predictions based on structural patterns documented in other North American desert rodent communities. Stated in null form, these were: (1) species richness and guild size are random variables; (2) species coexistence and body size are independent; (3) members of taxonomic-foraging guilds co-occur at random; and (4) guilds that co-occur more or less frequently than expected do not show dissimilarity in microhabitat use.

Methods

Study Area

This study was conducted in Capitol Reef National Park (CARE), in Wayne County, south-central Utah, USA (38° 15' N 111° 15' W), an area that typifies the Canyon Country Province of the Colorado Plateau. Topography of CARE is complex, composed of intricate canyon systems, slickrock cliffs and slopes, mesas, talus, benchlands, and alluvial floodplains. Elevations range from 1,195 to 2,690 m. A wide variety of edaphic conditions are present, including soils derived from volcanic, aeolian, and sedimentary parent materials. The climate is arid, temperate continental. Precipitation is distributed between winter snowfall and summer thunderstorms and averages 17 cm per year.

With respect to mammalian biogeography, CARE lies within the Canyonlands Province of the Colorado Plateau faunal area. The majority of species are drawn from Cosmopolitan and Chihuahuan aerographic faunal elements (Armstrong 1977). Distribution patterns within the Canyon Country Province largely reflect physical boundaries to animal movements, primarily major river systems and their canyons.

Rodent and Habitat Sampling

I sampled rodents and habitats at 104 study sites, representing grassland, shrubland, and woodland plant community types within the cold-temperate lowland zone (Spence et al. 1995). All sites were within a 40-km radius of CARE Park Headquarters and not isolated by significant barriers to rodent movement and dispersal, such as major rivers or mountain ranges. Therefore, I assumed that local biogeographic effects were minimal and that the rodent fauna at each study site was drawn from a common species pool.

Sampling was conducted in the fall of 1988–1991 (September–October). At each site, I established a rectangular 2 x 25 trap grid, with stations spaced

10 m apart. Three snap traps (two Museum Specials™ and one Victor™ rat trap) were placed within a 1 m radius of each station, and baited with a mixture of peanut butter, whole oats, and birdseed. Each grid was sampled for two days, with traps checked morning and evening. Analyses of preliminary trapping data indicated that this level of sampling effort was adequate to detect both species richness and relative abundance. Captured small mammals were identified to species, aged by pelage condition, and weighed using a hand-held Pesola™ scale. Voucher specimens were deposited with the Resource Management Office at CARE.

I described microhabitat characteristics at each small mammal capture location, by recording the presence or absence of microhabitat components within a 1 m radius of the trap. These components represented the primary structural habitat features present across the study area: herbaceous vegetation, low shrubs (<50 cm height), medium-stature shrubs (50–100 cm), tall shrubs (>100 cm), deciduous trees, evergreen trees, downed woody material, and rock outcrops.

Statistical Analysis

I followed Brown's (1973) criteria to minimize the influence of rare or transient individuals on estimates of rodent community parameters. Only common species (those comprising >5% of total individuals at a site) were included in the analyses, except for large rodents (>80 g), which are often under-represented because of trapping bias. I assigned each captured species to one of five guilds, based on taxonomy (Family) and diet (following Morton 1979).

Distributions of community parameters (numbers of species and guilds) were assessed by fitting observed values to a Poisson distribution. I used a chi-square goodness-of-fit test to detect significant ($P \leq 0.05$) deviations from randomness.

Body sizes of coexisting rodents were tested with null-model simulations, using the modified 2 x 2 contingency table procedure of Bowers and Brown (1982). Separate simulations were conducted for the subset of omnivorous species and for all species combined. I used a critical mass ratio value of 1.5, originally proposed by Brown (1973) as a conservative estimate of Hutchinson's ratio. I classified all coexisting and non-coexisting species pairs as having a mass ratio ≥1.5 or <1.5, calculated from the mean mass of adult individuals captured in this study. The simulation randomly shuffled observed data to create a new 2 x 2 table with the same marginal totals, from which I calculated:

$$Y^2 = \Sigma\,(S - E)^2/E,$$

where S was the number of pairwise occurrences in each cell and E was the expected value based on the marginal totals. This process was repeated 5,000 times to obtain a randomization distribution of Y^2 under the null hypothesis of independence. The locations of observed Y^2 values (calculated from capture data) within their respective randomization distributions, yielded an approximate probability of obtaining the observed values by chance alone.

I also used a null-model simulation to examine pairwise coexistence of desert rodent guild members. The simulation drew a random set of rodent pairs, equal in size to the original data set, by sampling with replacement from a pool containing all guilds, weighted by their respective number of members. Random pairs contained representatives of one or two guilds, except that single guild pairs could only be drawn from guilds containing >1 species. Occurrences of 13 possible guild pairs were tabulated and the process repeated 5,000 times, to derive randomization distributions of expected occurrence, under the null hypothesis of random association. The location of observed pairwise guild occurrence values within their respective randomization distributions reflected the approximate probability of occurrence by chance alone (Manly 1991). I applied a Bonferroni correction to maintain an overall Type I error rate of $P < 0.05$ for the 13 pairwise tests.

I tested for differences in microhabitat use among "significant" guild pairs (i.e., those that occurred more or less frequently than expected). I calculated pairwise microhabitat dissimilarity for all species, using the Bray-Curtis coefficient (Ludwig and Reynolds 1988). Differences in mean coefficient values between significant and non-significant guild pairs were compared with a randomization test (Manly 1991). I again applied a Bonferroni correction, to maintain an overall Type I error rate of $P < 0.05$.

Results

Species Richness

Species composition varied considerably across the 104 study sites. A total of 52 different species combinations were observed, the majority occurring only once or twice, and few occurring >3 times (Fig. 1). Species richness ranged from one to five per site, $\bar{x} = 2.1$. The majority of observed combinations contained two or three species (Fig. 2). This distribution approached non-randomness ($X^2 = 7.1$, $P < 0.10$).

Guild Structure

Five taxonomic-foraging guilds were represented: omnivorous Cricetids (5 species), omnivorous Sciurids (4 species), herbivorous Cricetid (1 species), insectivorous Cricetid (1 species), and granivorous heteromyid (2 species) (Table 1). Omnivorous Cricetids and granivorous heteromyids were most widely distributed, appearing in 83% and 44% of the observed species combinations, respectively (Table 1).

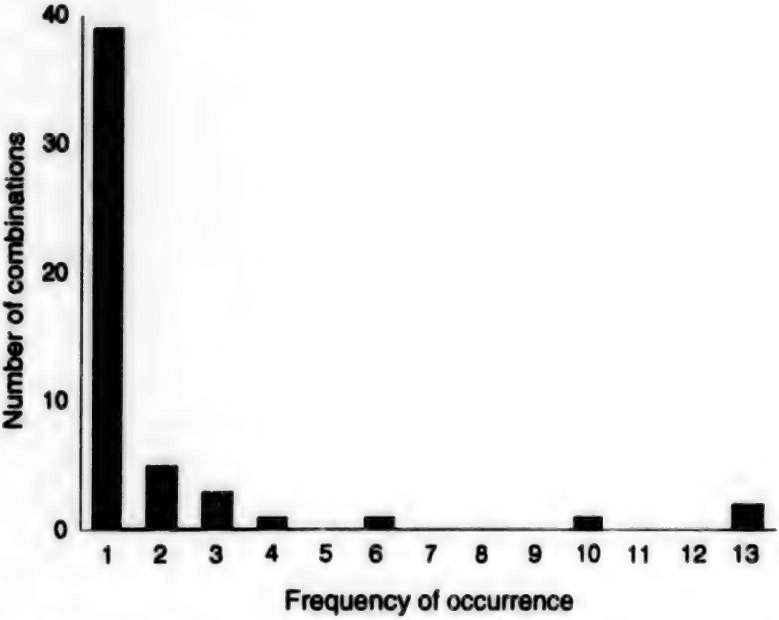

Fig. 1. Frequencies of occurrence of 52 desert rodent species combinations found at 104 sample sites in the Canyon Country Province, Colorado Plateau.

Most assemblages contained members of two guilds (Fig. 3). This distribution was significantly non-random ($X^2 = 10.89$, $P < 0.025$). There was considerable repetition of guild members, with 38–50% of all assemblages having >1 representative of a given guild.

Of 13 possible guild pairings, one occurred more frequently than expected and two occurred less frequently than expected. Omnivorous Cricetids occurred together more frequently than expected ($P < 0.0001$), while omnivorous Sciurids occurred together and in combination with omnivorous Cricetids less frequently than expected ($P < 0.0001$).

Body Size

Body size and coexistence were not independent among omnivorous species ($Y^2 = 3.5$[illegible]2). Species of similar body size (mass ratio <1.5) coexisted less frequently than expected, while species of dissimilar size (mass ratio ≥1.5) occurred more frequently than expected. This relationship disappeared when all other guilds (granivore, herbivore, and insectivore) were included in the analysis ($Y^2 = 0.06$, $P = 0.59$).

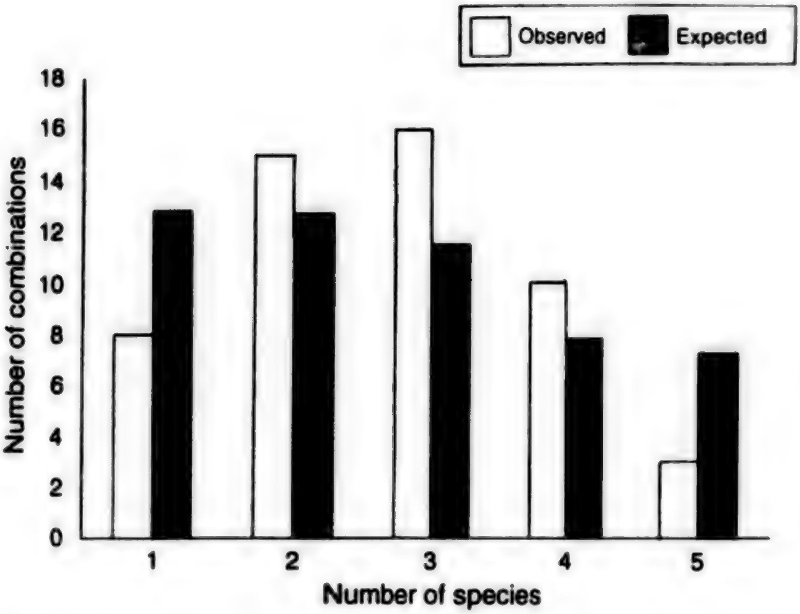

Fig. 2. Desert rodent species richness in 52 observed species combinations in the Canyon Country Province, Colorado Plateau. Expected values derived from Poisson distribution.

Microhabitat Use

Among the three guild pairs with observed occurrences significantly different than expected, only one showed differences in microhabitat use. Pairs of omnivorous Cricetids, which occurred together more frequently than expected, had significantly greater microhabitat dissimilarity ($P = 0.01$) than guild pairs with nonsignificant frequencies of co-occurrence (Table 2).

Discussion

Species Richness

Desert rodent assemblages of the Canyon Country Province showed a range of species richness similar to that reported from neighboring biogeographic regions, including the Chihuahuan Desert (Brown and Kurzius 1989), Mojave Desert (Hafner 1977), and Great Basin (Brown 1987), although mean values for my study sites were lower. I found spatial variation

Table 1. Taxonomic/foraging guilds represented in 52 observed small mammal assemblages in the Canyon Country Province, Colorado Plateau.

Guild	Member species	Frequency of occurrence[a]
Omnivorous Cricetid		83%
	brush mouse (*Peromyscus boylii*)	
	canyon mouse (*P. crinitis*)	
	deer mouse (*P. maniculatus*)	
	pinyon mouse (*P. truei*)	
	western harvest mouse (*Reithrodontomys megalotis*)	
Granivorous Heteromyid		44%
	Ord's kangaroo rat (*Dipodomys ordii*)	
	Great Basin pocket mouse (*Perognathus parvus*)	
Omnivorous Sciurid		35%
	cliff chipmunk (*Tamias dorsalis*)	
	Hopi chipmunk (*T. rufus = quadrivittatus*)	
	least chipmunk (*T. minimus*)	
	white-tailed antelope squirrel (*Ammospermophilus leucurus*)	
Herbivorous Cricetid		17%
	desert woodrat (*Neotoma lepida*)	
Insectivorous Cricetid		10%
	northern grasshopper mouse (*Onychomys leucogaster*)	

[a] Across all 52 observed species combinations.

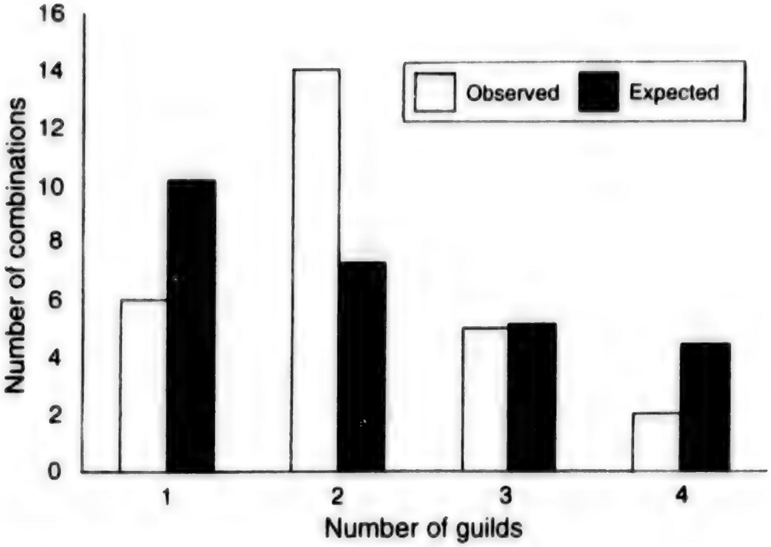

Fig. 3. Number of desert rodent taxonomic/foraging guilds represented in 52 observed species combinations in the Canyon Country Province, Colorado Plateau. Expected values derived from Poisson distribution.

Table 2. Microhabitat dissimilarity (Bray-Curtis coefficient, mean ± SE), of Canyon Country desert rodent guild pairs with occurrences significantly different than expected, compared to nonsignificant pairs. Asterisk indicates significant differences ($P < 0.05$).

Guild pair	Dissimilarity
Omnivorous Cricetids together	0.74 ±.02*
Omnivorous Cricetids + Sciurids	0.66 ±.02
Omnivorous Sciurids together	0.58 ±.03

Canyon Country desert rodent assemblages do have deterministic aspects. The number of observed species combinations was large, but much smaller than the total number possible. Observed combinations were also non-random with respect to the number of species and taxonomic/foraging guilds represented. These patterns are likely a consequence of processes documented in other desert rodent communities; for example, competition and responses to patchily distributed resources.

Guild Structure

Canyon Country desert rodent fauna showed more consistent structure when viewed at the guild level. Assemblages were relatively simple, often with more than one representative from the dominant guild (omnivorous Cricetids). These results suggest that multiple species are capable of filling the same roles in different assemblages. Functional similarity has been proposed as a cause of species mixes across various desert ecosystems (MacMahon 1976). In contrast to other biogeographic regions, Canyon Country desert rodent assemblages appear to have considerable redundancy of guild members, perhaps a consequence of the high macro- and microhabitat diversity. I found evidence both supporting and rejecting Brown's (1987) hypothesis that coexisting species tend to belong to different taxonomic and functional groups. The morphologically similar Cricetid rodents of the Canyon Country Province have apparently evolved mechanisms facilitating successful coexistence, while the Sciurids may not have.

Body Size

Cricetid-dominated desert rodent assemblages of the Canyon Country show body size relationships similar to those found among Heteromyid rodents in other North American deserts (Bowers and Brown 1982, Brown 1987, Reichman 1991). These results are in contrast to Price and Brown's (1983) observation that Cricetid rodent assemblages do not show distinct size divergence. My differing conclusions may reflect the fact that the assemblages they considered had too few Cricetids for such patterns to be detected. As in other North American deserts, morphological patterns of coexisting Canyon Country desert rodents are closely tied to guild structure and are most evident among the most abundant taxonomic group.

Microhabitat Use

Microhabitat use appears to be an important aspect of community organization among Canyon Country desert rodents. Dissimilarity was apparent only among sympatric omnivorous Cricetids. These differences likely serve to minimize competition and facilitate coexistence among a group of taxonomically related and morphologically similar species. Similar resource partitioning has been documented in other rodent assemblages with a large Cricetid component (Meserve 1976, Hallett 1982). Coexisting omnivorous Cricetids and Sciurids did not show significant microhabitat separation. However, these species likely avoid interference competition by temporal separation, the former group being nocturnal, and the latter primarily diurnal. In contrast, omnivorous Sciurids did not show significant differences in microhabitat resource use, nor did they co-occur at any study sites.

Acknowledgments

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Home Ranges and Movements of Pronghorn in Northern Arizona

Richard A. Ockenfels
William K. Carrel

Arizona Game and Fish Department
Research Branch
2221 W. Greenway Road
Phoenix, Arizona 85023-4312

Charles van Riper III

U.S. Geological Survey
Biological Resources Division
Colorado Plateau Research Station
P. O. Box 5614
Flagstaff, Arizona 86011-5614

Abstract. During October 1992, we captured 17 adult pronghorn (*Antilocapra americana*) within the environs of Wupatki National Monument (NM), Arizona, and 20 adults in or near Petrified Forest National Park (NP), Arizona. Each animal was relocated over the next two years to determine home-range sizes, movement patterns, and movement barriers. The greatest distance between any two consecutive locations was the only variable having a substantial effect on home-range size; neither animal gender or mean distance between locations added to the predictive ability. Multiple core use areas were more evident for females and their home ranges were significantly larger in Wupatki NM than in the Petrified Forest NP environs. Unfenced, 2-lane paved roads did not restrict pronghorn movements within either park, and no peak crossing periods were discernible. However, fenced, paved 2-lane roads and fenced, divided 4-lane highways outside of the parks constituted movement barriers. Furthermore, fenced railroad rights-of-way were barriers and influenced shapes of pronghorn home ranges. Pronghorn populations in northern Arizona can, therefore, be partially defined by highway and railroad barriers. These barriers could be modified to facilitate pronghorn interchange by either: (1) removing fencing; (2) expanding rights-of-way dimensions, then modifying fences; or (3) relocating rights-of-way out of pronghorn habitat. Knowledge of pronghorn home ranges and movements can be used to better manage populations, plan land uses, and mitigate human-related activities.

Key words: Antelope, *Antilocapra americana*, fences, geographic information systems, highways, home ranges, movements, Petrified Forest National Park, pronghorn, railroads, rights-of-way, Wupatki National Monument.

Pronghorn (*Antilocapra americana*) are a species of special concern in Arizona and intensified management is necessary to ensure that adequate populations are maintained throughout the state. Knowledge of pronghorn movement patterns is needed for effective land-use planning, mitigating effects of human-related activities, and practicing sensible game management (e.g., harvest rates).

In managing pronghorn, human-related activities are of concern because they can lower habitat quality (Neff 1986). With increased knowledge of pronghorn movements, land planners and managers can improve the design of developments, better place livestock water sources, and improve the design of fence placement. Pronghorn herd management strategies in Arizona are accomplished through hunt structures based on game management units (GMUs). Although natural landscape features are sometimes used to define GMU boundaries, more often boundaries are major roads.

In some areas, it is believed that highway and railroad fenced rights-of-way fragment pronghorn habitat and restrict movements, thereby isolating populations or preventing movements to seasonal ranges (Buechner 1950, O'Gara and Yoakum 1992, Ockenfels et al. 1994). Pronghorn are generally considered a nomadic animal, moving within habitats in response to changing conditions due to drought, winter storms, human disturbances, forage changes, and water availability (O'Gara and Yoakum 1992, Ockenfels et al. 1994). With increased habitat fragmentation, fewer pronghorn populations can respond to perturbations and maintain traditional migratory behavior (O'Gara and Yoakum 1992). Determining if highways and railroads are movement barriers can assist in better management of pronghorn populations.

This study was initiated to examine home ranges and movement patterns of pronghorn in two study areas in northern Arizona. Our objectives were to: (1) document pronghorn movement patterns; (2) determine home-range sizes for female and male adult pronghorn; (3) determine whether interchange occurred among neighboring herds; and (4) identify what types of barriers isolated pronghorn.

Study Areas

We chose two locations in northern Arizona, each delineated by a GMU and also centered around a national park. Our northeastern study area was most of GMU 2A that encompassed Petrified Forest National Park (NP) (Fig. 1). The north-central study area contained Wupatki and Sunset Crater National Monuments (NM) and encompassed most of GMU 7E (Fig. 2).

Northeastern Study Area

We centered our efforts south of I-40, in or near Petrified Forest NP, excluding lands administered by the Navajo Nation. Most of this area was

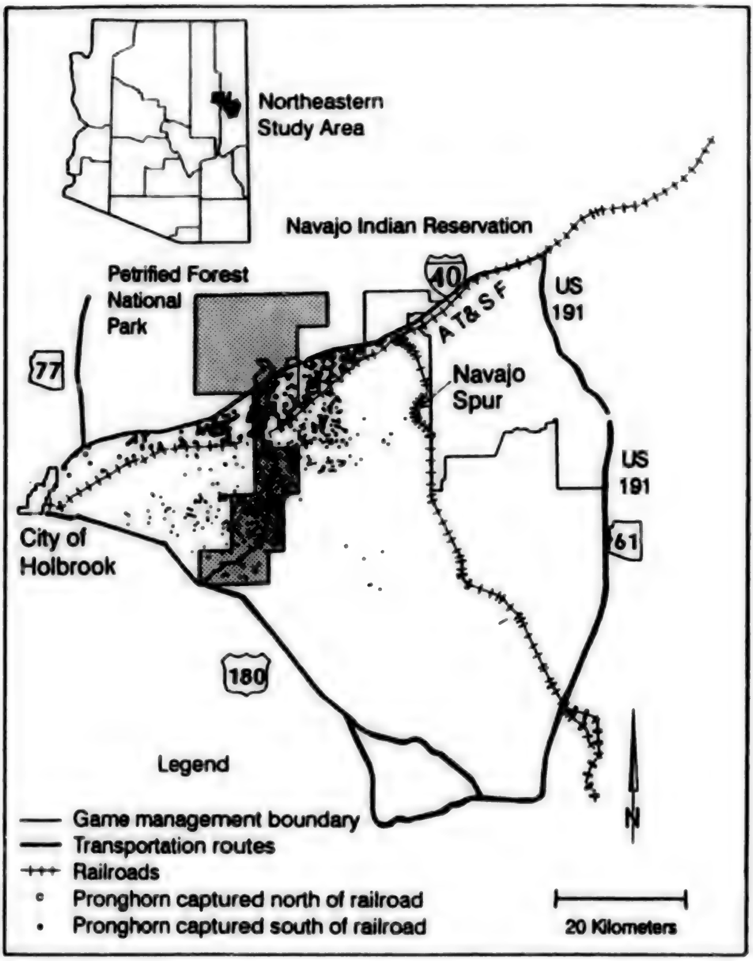

Fig. 1. Locations of radio-equipped adult pronghorn sightings, from 1992–94, within our northeastern Arizona study area. The study area was bounded by Game Management Unit 2A and centered on Petrified Forest National Park.

undulating terrain with rugged mesas or hills throughout, and numerous gullies extending from highly-eroded cliffs. Elevation ranged from 1,650 to 1,800 m. The Puerco River was the only major waterway but was not deeply incised.

This study area contained four sub-areas based on highways and railroads: (1) the area north of I-40 to the Navajo Indian Reservation; (2) the area between I-40 and north of the fenced Atchison, Topeka, and Santa Fe (AT&SF) railroad right-of-way; (3) the area south of the AT&SF right-of-way to U.S. 180 and east to the Navajo railroad spur line; and (4) the area east of the Navajo spur line (Fig. 1).

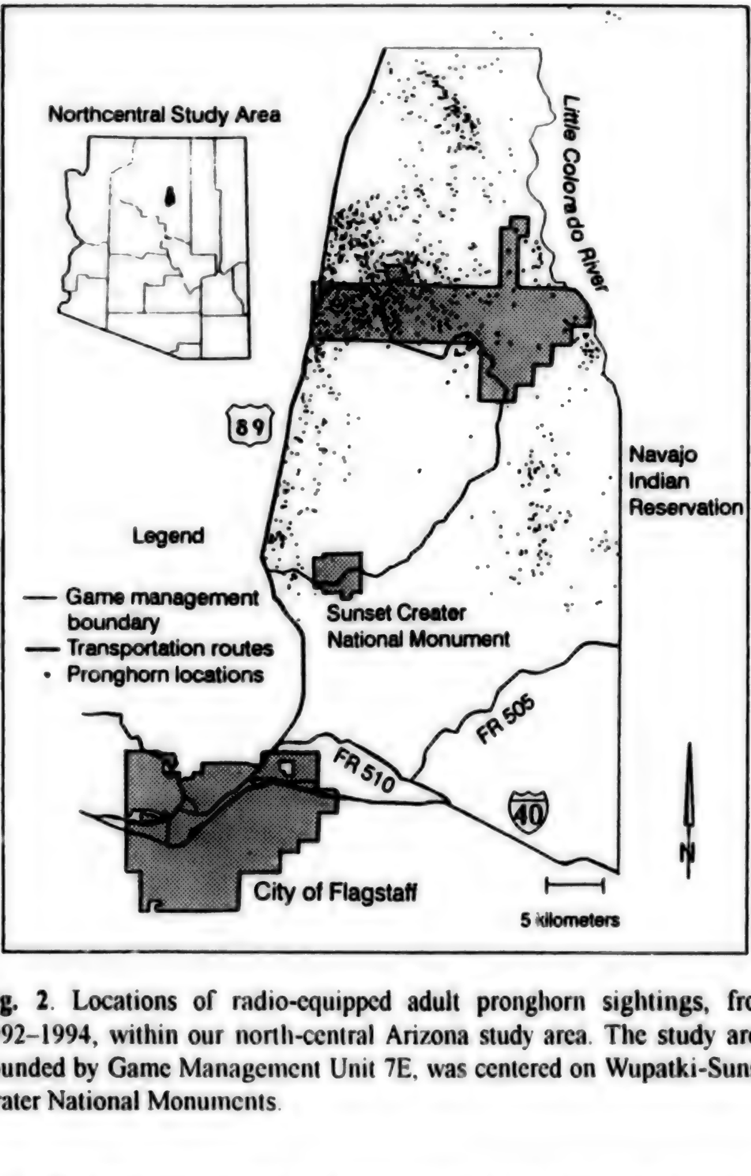

Fig. 2. Locations of radio-equipped adult pronghorn sightings, from 1992–1994, within our north-central Arizona study area. The study area, bounded by Game Management Unit 7E, was centered on Wupatki-Sunset Crater National Monuments.

Yearly precipitation was low (1941–1970: $\bar{x}$ = 18.7 cm), with over one-half of the rainfall occurring during brief thunderstorms in July–September (Sellers and Hill 1974). Average snowfall was only 12.4 cm, and snow seldom remained on the ground more than a few days.

Great Basin grassland (Brown 1994) and juniper (*Juniperus* spp.) woodland dominated the landscape. Blue grama (*Bouteloua gracilis*) and alkali-sacaton (*Sporobulus airoides*) were the predominant grasses. Sagebrush (*Artemisia* spp.), saltbush (*Atriplex* spp.), rabbitbrush (*Chrysothamnus* spp.), and Mormon-tea (*Ephedra* spp.) were scattered throughout, often forming small thickets. Snake-weed (*Gutierrezia* spp.) was abundant in localized poorer-condition sites. Plant nomenclature follows Kearney and Peebles (1960).

North-central Study Area

We selected this study area east of U.S. 89 (Fig. 2). Elevation ranged from 1,350 m along the Little Colorado River to 2,700 m at Sunset Crater NM. Undulating terrain throughout the area was broken by volcanic cinder hills and lava flows.

Because of the wide elevational range, climate in this area varied considerably. In the low-elevation northern portion, precipitation was low (1956–1962: $\bar{x}$ = 13.1 cm), with some December–January snowfall ($\bar{x}$ = 21.8 cm). Because of the presence of the nearby San Francisco Peaks, snowfall in the southern portion was substantially greater, resulting in extensive snow cover. Summer (July–September) rainfall in the southern portion was more consistent than in the northern portion, and year-round precipitation was greater (Flagstaff 1950–1970: $\bar{x}$ = 50.3 cm).

A short-grass prairie of *Hilaria* spp. and alkali-sacaton predominated the northern portion of this study area (Brown 1994). The southern portion was predominantly Rocky Mountain Coniferous Forest (Brown 1994), which was comprised almost entirely of ponderosa pine (*Pinus ponderosa*). Juniper woodlands occupied most of the eastern edge, as well as a band between the pine forest and short-grass prairie. Localized, dense stands of cliffrose (*Cowania mexicana*) and Apache plume (*Fallugia paradoxa*) occurred in the juniper woodlands.

Methods

Capture and Location

Using a net-gun fired from a helicopter (Firchow et al. 1986), we captured adult pronghorn in mid-October 1992. All animals were radio-equipped, ear-tagged, and released at their capture sites. In the northeastern study area, we captured pronghorn on and near Petrified Forest NP, but only in sub-areas south of I-40 and west of the Navajo spur line (Fig. 1). At our north-central study location, we captured pronghorn on or near Wupatki NM, all east of U.S. 89 and north of U.S. Forest Service roads (FR) 510 and 505.

We aerially located pronghorn two to three times per month, between October 1992 and September 1994, from various modified, high-wing, single engine aircraft. Each aircraft had a forward-phased, twin-Yagi antenna array mounted to the wing struts for signal detection and general signal direction, and a rotatable, belly-mounted, two-element antenna used to pinpoint pronghorn locations (Carrel 1972a,b). During flights, we plotted animal locations on U.S. Geological Survey (USGS) 7.5-min topographic maps. After each flight, Universal Transverse Mercator (UTM) coordinates for each location were defined to the nearest 0.1 km.

We also located pronghorn one to two times per month on the ground using a handheld two-element antenna. The UTM coordinates were derived to the nearest 0.1 km from USGS 7.5-min maps; we also used a Global Positioning System (GPS) receiver to calculate coordinates. After encoding and verifying the data, we merged ground and aerial locations, then transferred the UTM-coordinate files into a Geographic Information System (GIS).

Data Analysis

Statistical significance was set at alpha = 0.10. We decreased chances of accepting a false null hypothesis (Type II error) by choosing 0.10 instead of 0.05, but increased the probability of rejecting the null when it was indeed true (Type I error; Zar 1984). To provide management recommendations, with anticipated small sample sizes, we deemed Type II errors more important than Type I. Statistical tests were performed with SPSS/PC+ software (Norusis 1990).

Movements

Using features in HOME RANGE (Ackerman et al. 1990), we calculated (in km) the distance between consecutive locations and mean distance for each animal (which we defined as a movement). For each animal, we counted the number of movements >10 km and >20 km, and also recorded the largest movement and date (month, day, year) of that completed move.

Frequency distributions of movement variables ($\bar{x}$ distance, ≥10 km, ≥20 km, greatest distance) were assessed for normality with Kolmogorov-Smirnov (K-S) one-sample tests (Zar 1984). For descriptive purposes, we calculated gender-specific descriptive statistics ($\bar{x}$, SD, range) for normally-distributed variables in each study site, then pooled data and calculated descriptives for all adult pronghorn.

We tested for study site or gender-related differences, as well as site x gender interactions, in mean distance and greatest distance moved with 2 x 2 analysis-of-variances (ANOVAs). ANOVA was used because we were simultaneously testing >2 categories of normally distributed variables. Within study sites, we used *t*-tests for gender comparisons.

A Mann-Whitney (M-W) comparison was utilized for gender-related differences in long distance movements. The numbers of movements ≥10 km were not normally distributed, so a 2-group rank test had to be used. We also used a M-W comparison to test if site affected the number of movements ≥10 km made by females.

Rights-of-way Crossings

To determine if pronghorn crossed unfenced roads and highway or railroad rights-of-way, using GIS, each study area was subdivided by fenced rights-of-way and park roads. We then overlaid locations on this sub-area cover to match each location. Lastly, we sorted the file by animal identification and date, counting movements between appropriate sub-areas. For each study area, we summed the crossings by gender for each month from October 1992 to September 1994.

The 100% minimum-convex polygon method was selected as our estimate of home-range size, using a 50% convex polygon as the estimate of core (high use) areas (Ackerman et al. 1990). For each site, we calculated gender-specific descriptive statistics ($\bar{x}$, SD, range) for home-range and core use sizes, and assessed frequency distributions of home-range and core area size for normality with K-S one-sample tests. We then pooled the data and calculated descriptives for all adult pronghorn. We tested for site or gender-related differences, as well as site x gender interactions, in home-range and core use size with 2 x 2 ANOVAs. As with movement data, we used t-tests within each site for gender-related comparisons.

To determine significant factors affecting home-range size, we plotted all variables against each other, ran a correlation matrix, then used forward, step-wise regression.

Results

Capture and Location

In our northeastern study area, we captured, radio-collared, and ear-tagged 20 (15F, 5M) pronghorn. Four does were captured north and the remaining 16 pronghorn south of the AT&SF right-of-way. These animals were relocated 1,736 times (Fig. 1). Most locations were during daylight, between 0500 and 2000 Mountain Standard Time (MST).

We captured, radio-collared, and ear-tagged 17 (13F, 4M) adult pronghorn in the north-central study area. Five animals (4F, 1M) were captured within Wupatki NM, the rest captured to the north. We relocated these animals 1,671 times over the next two years, mostly between 0500 and 2000 MST (Fig. 2).

General Movements

Normality tests indicated that long distance movements were not normally distributed, whereas mean distance and greatest distance between any two consecutive locations were likely sampled from normally-distributed populations (Table 1).

Table 1. Movement and home-range characteristics of adult pronghorn in two areas of northern Arizona, 1992–1994.

Variable	Northeastern study area		North-central study area		
	Females	Males	Females	Males	Overall
n	15	5	13	4	37
Mean distance[a]	3.3	2.7	3.4	3.1	3.2
SD	0.6	0.4	0.5	0.5	0.6
Range	2.5–4.4	2.0–2.9	2.5-4.0	2.4–3.6	2.0–4.4
Number of movements ≥10 km[b]	36	7	66	4	113
Number of movements ≥20 km[b]	3	0	5	2	10
Mean of greatest distance[a]	14.4	9.0	16.8	13.2	14.4
SD	8.0	2.0	6.4	7.1	7.0
Range	6.0–35.0	6.5–10.6	7.6-33.7	7.8–22.8	6.0–35.0
Mean home-range size (km^2)[c]	124.0	81.7	195.2	135.6	144.6
SD	59.6	40.9	130.1	59.4	95.7
Range	56.5–243.2	44.4–140.0	80.5-552.0	72.8–211.1	44.4–552.0
Mean core use area (km^2)[c]	21.2	9.2	36.7	27.7	25.7
SD	5.4	7.4	25.4	31.9	20.2
Range	9.7-28.1	2.1-20.6	16.1-104.7	7.7–75.0	2.1–104.7

[a] Km between two consecutive locations for each animal as calculated by HOME RANGE (Ackerman et al. 1990), then averaged for mean distance.

[b] Distance between two consecutive locations.

[c] Home-range size using 100% minimum convex polygon and core use area using 50% minimum convex polygon from HOME RANGE (Ackerman et al. 1990).

Mean movements did not differ ($F = 1.01$; df = 1,36; $P = 0.321$) by site, but did ($F = 5.34$; df = 1,36; $P = 0.027$) by gender (Table 1); females ($\bar{x}$ = 3.3 km, SD = 0.5, $n = 28$) tended to move more in their home ranges than did males ($\bar{x}$ = 2.9 km, SD = 0.5, $n = 9$). No site x gender interactions were observed ($F = 0.72$; df = 1,36; $P = 0.404$). Much of the gender-related difference can be explained by a correlation ($r = 0.64$, $n = 37$, $P < 0.001$) between mean movements and greatest movements.

We found no difference ($F = 1.54$; df = 1,36; $P = 0.224$) in greatest movements for the two study sites, but greatest movements differed ($F = 3.03$; df = 1,36; $P = 0.091$) by gender (Table 1); females ($\bar{x}$ = 15.5 km, SD = 7.3) had larger maximum movements than males ($\bar{x}$ = 10.9 km, SD = 5.1). As with mean movement, there was no site x gender interaction ($F = 1.59$; df = 1,36; $P = 0.719$).

Females had more (M-W $Z = -2.01$, $P = 0.045$) movements $\geq$10 km than males. Few females or males had movements $\geq$20 km. Females in the north-central site had more (M-W $Z = -1.95$, $P = 0.051$) movements $\geq$10 km than females in the northeastern site.

Specific Movements Within Study Areas

For the 20 adult pronghorn captured in the northeastern site, females tended to move more ($t = 2.26$, df = 18, $P = 0.036$) than males, and greatest movements of females were more variable and exceeded ($t = 2.41$, df = 17.63, $P = 0.027$) those of males (Table 1). Most (65%) pronghorn made some movements $\geq$10 km, however, only 15% made infrequent movements $\geq$20 km.

The greatest single movement was 35.0 km, made between 10 and 17 May 1993, by a doe north of the AT&SF railroad right-of-way. Overall, this doe ranged east-west from the community of Navajo nearly to Holbrook (Fig. 1). A doe south of the right-of-way moved 28.3 km (prior to 5 May 1993).

Of the 17 adult pronghorn in the north-central site, females did not ($t = 0.93$, df = 15, $P = 0.393$) move about more than males, nor did female greatest movements exceed ($t = 0.94$, df = 15, $P = 0.363$) those of the males (Table 1). Most (76%) pronghorn exhibited at least some movements $\geq$10 km. Only 3 (17.6%) had movements $\geq$20 km, and these were infrequent (only 2–3 times). Unlike the northeastern location, where only females ($n = 3$) moved long distances, one male and two females in the north-central location had movements $\geq$20 km. One female moved 33.7 km between 31 March and 3 April 1993.

Rights-of-way Crossings

Crossings, by both females and males, of the paved but unfenced road in Petrified Forest NP occurred throughout the two years of this study (Fig. 3).

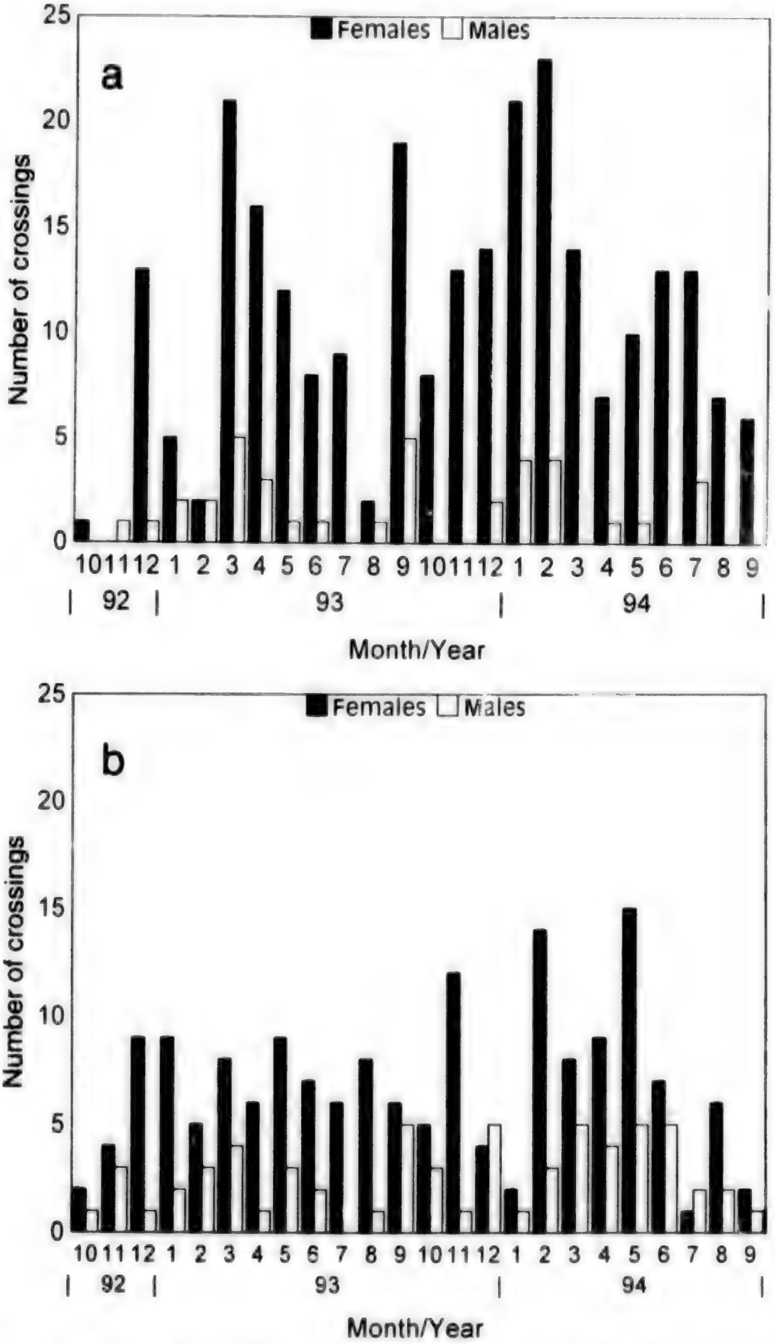

Fig. 3. Number of crossings during 1992–1994, by adult radio-equipped pronghorn, of unfenced, paved roads at (a) Petrified Forest National Park and (b) Wupatki National Monument.

No discernible crossing peak by either females or males was evident. Relative to the number captured, neither females or males seemed to cross more readily. Only two of the 15 females never crossed the road; one always stayed to the east, the other to the west. During the two years of this study, no females or males in the northeastern site crossed paved highways that were fenced (Fig. 1). Many pronghorn locations were within one km of I-40, US 191/AZ 61 and US 180, but no animals crossed. In fact, some of the home ranges seemed bounded by the roads. In addition, no crossings of the AT&SF or Navajo spur railroad rights-of-way were recorded (Fig. 1). For example, pronghorn captured north of the AT&SF had home ranges bounded by the railroad right-of-way and I-40, resulting in linear shapes, while those captured south of the railroad had non-linear home range shapes.

In our north-central study area, we documented 165 crossings of the paved, unfenced Wupatki NM road by females during the two years (Fig. 3b). One doe crossed a minimum of 46 times, including at least once in 21 of 24 months. Crossings occurred during all months and seemed to peak in winter and early spring of 93–94. For males, crossings ($n = 65$) occurred throughout the study by two of four bucks; one buck crossed a minimum of 44 times. One doe crossed the Little Colorado River, twice moving in the early spring onto the Navajo Indian Reservation to fawn (Fig. 2). No crossings of US 89 were documented, although numerous pronghorn locations were within 1 km of the fenced highway (Fig. 2).

Home Ranges and Core Use Areas

Home-range sizes clustered in the 75–125 km^2 range (Fig. 4). Few home ranges encompassed <50 km^2, and the three home ranges >250 km^2 were for females that had made large-scale seasonal movements. Core use areas were much smaller (Fig. 4). Home range and core use distributions were sampled from normal distributions (Table 1).

Home-range sizes varied by study site ($F = 5.05$; df = 1,36; $P = 0.031$), but not by gender ($F = 2.09$; df = 1,36; $P = 0.158$). Home-range sizes and variability were larger ($t = 2.15$, df = 22.32, $P = 0.042$) in the north-central study area than in the northeastern site (Table 1). There was no ($F = 0.06$; df = 1,36; $P = 0.805$) site x gender interaction in home-range size.

Similarly, core size varied by site ($F = 7.02$; df = 1,36; $P = 0.012$), but not by gender ($F = 2.23$; df = 1,36; $P = 0.145$). As with home-range size, core size and variability were larger ($t = 2.48$, df = 18.42, $P = 0.023$) in the north-central site than in the northeastern site (Table 1). There was no ($F = 0.04$; df = 1,36; $P = 0.844$) site x gender interaction.

The correlation between core and home-range size was only moderate ($r = 0.56$, $n = 37$, $P < 0.001$). Apparently other factors were influencing home-range size in our study areas. A forward, step-wise regression ($F = 71.98$; df = 1,35; $P < 0.001$) indicated that the greatest movement value was the only substantial variable affecting home-range size ($r^2 = 0.67$). Neither

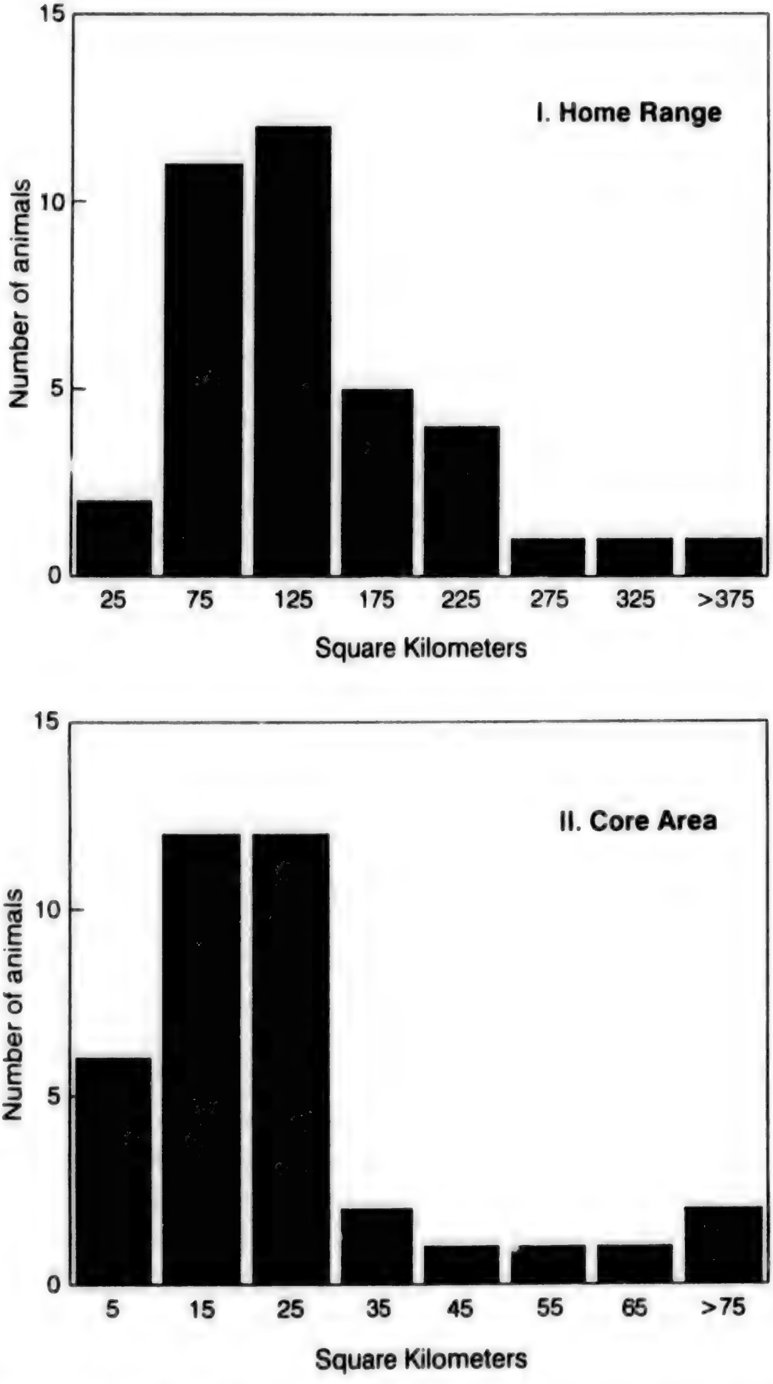

Fig. 4. Adult pronghorn (I) home-range and (II) core area sizes, in the northeastern and north-central Arizona study areas, 1992–1994.

the number of locations or gender added to r^2 nor did the mean distance between locations. However, when home range boundaries delineated by HOME RANGE, were overlaid with locations, most suggested fairly uniform movements throughout the home ranges.

The greatest influence on home range shapes of the pronghorn at both study areas was human-related development, particularly fenced highways and railroad rights-of-way.

Discussion

In our discussion we will deal with three major topics. First, we compare movements and home ranges between our study animals, then with findings from other areas of Arizona and the western United States. Secondly, we discuss what did, or did not, constitute a movement barrier. The third topic will deal with management actions that can be taken from the results of our research.

Movement and Home Range Comparisons

Movements

Mean pronghorn movements were not significantly different between our study sites. Furthermore, Ockenfels et al. (1994) found similar movement distances of pronghorn in central Arizona. There is nothing in the literature to indicate that mean movements (between relocation) in Arizona were different from pronghorn elsewhere. The nature of the species likely dictates at least a certain amount of movement to obtain daily requirements. These requirements should not differ substantially because of area if habitat conditions are reasonable.

Some of the differences in movements that we found between sites and gender can be accounted for by climatic influences. Pronghorn in our north-central study area were exposed to a regime of more variable precipitation and snowfall. Therefore, those pronghorn would sometimes have to move seasonally to prevent winter kill. This situation did not occur in our northeastern site, nor in central Arizona (Ockenfels et al. 1994). Historically, pronghorn in the north-central site used the higher elevations near Flagstaff for fawning and summer range. With human encroachment in many high elevation parks and meadows, suitable summer range areas have been reduced east of US 89. Recruitment into this pronghorn population could, therefore, be adversely affected by the loss of quality fawning and summer range.

The older age of pronghorn males captured in this study, particularly at the northeastern site, could be a significant factor in why gender-related movement differences were observed. Similar to central Arizona, young males tend to move more than mature, territorial individuals (Ockenfels et al. 1994).

Young males are often found in doe bands, and thus their movements are similar. Particularly during the breeding season, mature males move very little. With older males radio-collared in our study, one would expect less movement of this sex because of territorial constraints.

One other factor that contributed to movement differences between sites was the availability of permanent water sources. At our northeastern study site, the Puerco River provided permanent water throughout the year, especially within Petrified Forest NP. However, at the north-central site, there was no permanent water within Wupatki NM and pronghorn had to leave the park for livestock water sources to the north.

Home Range Comparisons

Pronghorn in our north-central study area had significantly larger home ranges than the northeastern animals. Weather certainly had an influence, as many of the north-central animals summered at higher elevations. However, lack of permanent water in the middle of our north-central study area (i.e, Wupatki NM), was probably a major contributing factor to the increase in home-range sizes. Ockenfels et al. (1994) showed that in central Arizona, water played a role in pronghorn home-range sizes. In fact, water in the West has a profound seasonal effect on the distribution of pronghorn (O'Gara and Yoakum 1992, Clemente et al. 1995).

Movement Barriers

Fenced Highway Rights-of-way

Buechner (1950), working in Texas, observed the negative effect highway rights-of-way fences had on pronghorn movements. White (1969) demonstrated that fenced highways blocked the movements of pronghorn in northern Arizona during a severe winter storm, resulting in losses of as much as 80% of some herds. In central Arizona, Ockenfels et al. (1994) provided further evidence of substantial fragmentation of pronghorn habitat and isolation of pronghorn herds by fenced highways.

After observing similar fragmentation in our study in northern Arizona, we are left to believe that rights-of-way fences are the major factor affecting pronghorn movements across their range.

Fenced Railroad Rights-of-way

Two transcontinental railroads traverse the entire width of Arizona. The AT&SF roughly follows the 35th parallel of northern Arizona, crossing much suitable pronghorn habitat. In addition to the two transcontinental lines, Arizona has many local rail lines, some of which could be in pronghorn habitat. In our northeastern study area, we demonstrated that pronghorn were isolated into two populations by the AT&SF. Similar fragmentation probably occurs in many other areas in the state and throughout the West, particularly if the tracks are tightly fenced on both sides.

Unfenced Rights-of-way

Although considerable traffic occurred seasonally on Petrified Forest NP and Wupatki NM roads, these unfenced paved roads did not adversely affect the movement patterns of pronghorn during the two years of our study. Ockenfels et al. (1994) observed similar patterns relative to certain roads (e.g., Dugas Road) in central Arizona. Thus, for management purposes, mitigation efforts should concentrate on fenced rights-of-way. Nonetheless, preventing any fencing of unfenced roads, highways, and railroads should also be of paramount concern for resource managers.

Management Implications

Fragmentation of habitat by fenced rights-of-way impairs movement of pronghorn in northern Arizona and probably affects survival and genetics of those herds. To facilitate movement and interchange among herds, it is imperative to reduce the effect of fenced rights-of-way on pronghorn populations. The pronghorn can then freely move as perturbations occur. Survival rates and genetic flow likely would increase. Winter kills, as a result of fenced rights-of-way blocking seasonal movements from severe storms (e.g., White 1969), could be mitigated with reasonable intervention.

Possible mitigation features could be: (1) removing fences along rights-of-way; (2) expanding rights-of-way dimensions by placing fences further away from the road or railroad, then modifying the fences to permit better movement of pronghorn between fenced areas (O'Gara and Yoakum 1992, Ockenfels et al. 1994); or (3) relocating rights-of-way out of pronghorn habitat. The use of underpasses has been found not to be an effective pronghorn management tool (Ward et al. 1980). In some areas, emergency plans could be established to remove fences during periods of severe weather to allow movement to and back from lower elevation habitats. To do so effectively, however, would require extensive knowledge of pronghorn movement corridors.

Arizona's current survey and harvest management program for pronghorn is designed around GMUs, most of which have been in existence since 1958. Many of the boundaries delineating these GMUs were based on highway rights-of-way. Because of the absence of movement across fenced right-of-ways observed during our study, some GMUs contain multiple pronghorn populations because of multiple fenced highway rights-of-ways within their boundaries. For example, GMU 7 is divided into 7E and 7W (by US 89) for some hunts, but typically not for pronghorn. Yet our results point out that animals do not interchange between 7E and 7W. Thus, isolated populations occur and combined survey and harvest data would not accurately reflect true pronghorn populations. Similar situations probably occur in other areas of the state, and perhaps throughout the West. If GIS methodology could be used to estimate the extent of the problem, pronghorn management strategies could be modified to better accommodate such fragmentation.

Acknowledgments

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Inventory of Bats in High Plateau Forests of Central and Southern Utah

Dan A. Foster[1]
Laura Grignon[2]
Evan Hammer[3]
Brian Warren[3]

National Park Service
Bryce Canyon National Park
Bryce Canyon, Utah 84717

Abstract. Bats utilizing water sources within plateau forests were surveyed at 24 sites in southern and central Utah. Fourteen taxa were captured, with eight of these formerly listed by the U.S. Fish and Wildlife Service as Category 2 species. The first documented capture of *Euderma maculatum* from the Manti-LaSal Mountains is noted.

Key words: Bats, forests, survey, water.

Information on presence/absence or distribution of bat species in forested areas of south and central Utah is incomplete. Of the bat species known to occur in Utah, 16 have the potential to inhabit high plateau forested areas (Hasenyager 1980). Concerns about possible declines in bat populations prompted the listing of 10 Utah species of bats as Category 2 candidate species in the fall of 1994 by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 1994). This classification is no longer used by the U.S. Fish and Wildlife Service and such species may now be called species of special concern.

A variety of land management practices such as timber harvest, abandoned mine reclamation, and recreation use may impact these taxa, thus necessitating further understanding of bats and their habitats in the region.

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[1] Present address: Nez Perce National Historical Park, Spalding, Idaho 83540.

[2] Present address: Department of Botany, North Carolina State University, Raleigh, North Carolina 27695.

[3] Present address: Department of Geography, University of North Carolina, Chapel Hill, North Carolina 27514.

A cooperative effort between Bryce Canyon National Park, Dixie National Forest, Fishlake National Forest, Manti-La Sal National Forest, and the National Biological Service was undertaken in 1995 to inventory bat species in high plateau forests.

The project had the following objectives:

1. determine presence/absence of bat species on forested lands in areas of potential water use,
2. obtain information on relative abundance of species present,
3. identify habitat types surrounding water sources, and
4. establish better working relationships between agencies for managing appropriate habitat.

The results from this research were intended to aid in understanding bat species occurrence and habitats used, allowing formulation of inter- and intra-agency efforts to protect and manage appropriate habitat for bat species.

Methods

The project was coordinated by the Division of Resource Management staff at Bryce Canyon National Park. Surveyors were volunteers and Bryce Canyon National Park staff. They were trained by personnel from the National Biological Service.

Survey sites (water sources) were determined in joint consultation among resource managers of the four management agencies. Due to the amount of area covered by the study (approximately 4.8 million acres) and the survey time available, each participating area was allotted six sites to be surveyed. Additional sites were identified if the initial six proved unacceptable. Hence, 24 sites were selected, with the intent to visit each two times in the survey season.

Site characteristics and conditions varied and changed throughout the season. Therefore, the actual location of the inventory site was determined in the field by the survey crew. Some sites were inaccessible early in the season due to snow or road condition, while others proved too large in surface area for effective coverage by mist nets. The field crew was given latitude to move the site to pre-selected alternative areas when necessary.

The two methods chosen for survey were mist netting and echolocation detection. Mist nets were set up approximately 30 minutes prior to sunset and monitored for at least 3 hours. The nets used were 50 denier, 1 ½" mesh, in 18, 30, and 42 foot lengths. A Titley Anabat II was used for determination of echolocation signals of bats in flight. We also made 15-minute taped recordings at each site during peak activity. These recordings will aid in the building of time-frequency diagram (sonograms) libraries for future research purposes. Echolocation detecting equipment provides the ability to monitor bat activity at the site, but species identification must be based on sonograms available for comparison (Toone 1994). Sonograms are being developed for the species in this study from recordings, but we were not able to make total use of this tool at this time. The major drawback to monitoring echolocation signals is the inability to differentiate between a single bat passing over many times or several bats passing a few times.

Brief descriptions of the area surrounding the net sites were included on field forms developed by the National Biological Survey. Information such as slope, aspect, elevation, and dominant vegetative cover in both distribution and height was described.

Results

A total of 238 bats were netted, representing 14 species, including eight species formerly listed Category 2 by the U.S. Fish and Wildlife Service. Appendix A lists the sites surveyed by cooperating agency with land management responsibility and the species and number of individuals captured at each location. A general list of the species netted in the study area includes:

Myotis californicus	California myotis
Myotis ciliolabrum[a]	western small-footed myotis
Myotis evotis[a]	long-eared myotis
Myotis lucifugus	little brown bat
Myotis thysanodes[a]	fringedmyotis
Myotis volans[a]	long-legged myotis
Myotis yumanensis[a]	Yuma myotis
Lasiurus cinereus	hoary bat
Lasionycteris noctivagans	silver-haired bat
Eptesicus fuscus	big brown bat
Euderma maculatum[a]	spotted bat
Idionycteris phyllotis[a]	Allen's big-eared bat
Antrozous pallidus	pallid bat
Nyctinomops macrotis[a]	big free-tailed bat

[a] Former U.S. Fish and Wildlife Service Category 2 species.

A vegetation classification of each survey site is also presented in Appendix B, according to the Spence/Romme/Floyd-Hanna/Rowlands (SRFR) classification (Spence et al. 1995) for the Colorado Plateau.

Discussion

No single method for determining the presence or absence of bat species has come to the forefront as the best (Thomas and La Val 1988). Capture by mist net allowed us to make positive identification of species, but included a bias from netting at water locations. It has been shown that at habitual drinking locations bats have a higher incidence of capture than at infrequently used watering locations (Kunz and Brock 1975). Bats using habitual flyways and watering sources may become accustomed to their surroundings and although echolocating, probably pay little attention to weaker echoes of nets and other traps (Thomas and West 1989), making them more susceptible to capture. Species that continually move roost, feeding, and watering sites may reduce their familiarity with a single location and decrease their susceptibility of capture, due to increased awareness of surroundings. Other biases introduced by use of mist net capture include: (1) visually oriented bats may be adept at avoiding nets; (2) different species forage and water in different manners; and (3) environmental conditions may limit bats encountered (Kunz and Kurta 1988). Mist nets also have the limitation of only sampling those bats flying at net height. Therefore, our capture of bats at watering locations may not be an accurate inventory of all the bats utilizing each habitat.

Comparison of our findings may be correlated to other studies and reports of habitat utilizations to corroborate habitat usage in the areas of our studies.

We were able to determine the presence of a variety of species on forest lands in the study area. Abundance of individual species would be inappropriate to speculate on based on the number of sites surveyed and the biases already discussed. Some interesting information did, however, come to light. First, silver-haired bats, long-legged myotis, long-eared myotis, and big brown bats were the most frequently netted bat species. These species seem to be common users of water at most sites; however no attempt at population trends can be made here. The second interesting find is species that were captured at only one net site in the study were *Yuma myotis*, Allen's big-eared bat, pallid bat, and big free-tailed bat. The latter three are more common in lower, warmer elevations than in the forested areas surveyed, but many factors may account for isolated occurrences of an individual species such as elevation, temperature, microhabitat, and so forth. Third was the capture of spotted bats in the Manti-LaSal Mountains. These are the first documented captures of spotted bats in this mountain range and two of the females captured were lactating, indicative of breeding in the area by this species (M. Bogan, National Biological Service, Albuquerque, New Mexico, personal communication). Appendix B provides a simplified listing of the habitat types surrounding the water sources where bats were identified. However, we recognize that use of the surrounding habitats was not determined. Species abundance and specific habitat use could only be determined by detailed, site-specific studies which include identification of roost sites and counting of individual animals for population estimates.

This study was a multi-agency cooperative effort. Continued coordination between the agencies involved in the management and protection of habitat for various bat species should be enhanced by the ground work laid by this project. This is important in that resources that cross management boundaries are shared and, therefore, must be managed by cooperative efforts and understanding.

Acknowledgments

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Appendix A. Species and numbers netted by survey site.

Net site	Numbers of species netted using the accompanying list													
Bryce Canyon National Park	1	2	3	4	5	6	7	8	9	10	11	12	13	14
East Creek		1	6			10	2		9	6				
Mossy Cave		2	1			4			10	1				
Swamp Canyon		2				4		1						
Bryce Creek		13	1			4			2					
Yovimpa Pass		1			1	1			2					
Hatch Pond			1											
Dixie National Forest	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Crawford Canyon	1[a]	1[a]	5			1		1						
Blubber Creek		1	1						4	8				
Yankee Meadow														
Leeds Creek									2					
Blue Spruce	1[a]	1[a]				1			1					
Tantalus Creek			1						4			2	4	
Fishlake National Forest	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Burnt Flat			1	1										
Forshea Spring				2		1			2	3				
Seven Mile Creek						1								
Eldridge Hollow									4	1				
Pahvant Road									1					
Beaver Valley														
Big Flat[b]														

Appendix A. *Concluded.*

Net site	Numbers of species netted using the accompanying list													
Manti-LaSal National Forest	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Lake Hill														
Elk Ridge	1	3	4			3		1	23	9	1			
Huntington Canyon						1		1	18	1				
Warner Lake			1			3		3	2	1	1			2
Deer Springs														
Medicine Lake[b]		2		4	2			4						
Pigeon Creek														

[a] Individual bat was either *Myotis californicus* or *Myotis ciliolabrum*

[b] Moved from the preceding location due to dry conditions

Species list for Appendix A

1. *Myotis californicus* (California myotis)
2. *Myotis ciliolabarum* (Western small-footed myotis)
3. *Myotis evotis* (Long-eared myotis)
4. *Myotis lucifugus* (Little brown bat)
5. *Myotis thysanodes* (Fringed myotis)
6. *Myotis volans* (Long-legged myotis)
7. *Myotis yumanensis* (Yuma myotis)
8. *Lasiurus cinereus* (Hoary bat)
9. *Lasionycteris noctivagans* (Silver-haired bat)
10. *Eptesicus fuscus* (Big brown bat)
11. *Euderma maculatum* (Spotted bat)
12. *Idionycteris phyllotis* (Allen's big-eared bat)
13. *Antrozous pallidus* (Pallid bat)
14. *Nyctinomops macrotis* (Big free-tailed bat)

Appendix B. *Survey locations and characteristic plant species.*

Site	Elevation	SSRFR formation	Characteristic species
Bryce Canyon National Park			
East Creek	7900'	montane grassland	Grass spp./*Artemisia nova*/*Pinus ponderosa*
Mossy Cave	6830'	montane forest and woodland	*Pinus edulis*/*Juniperus scopulorum*
Swamp Canyon	7120'	montane forest and woodland	*Quercus gambelii*/*Juniperus scopulorum*
Bryce Creek	6840'	montane forest and woodland	*Pinus edulis*/*Juniperus scopulorum*
Yovimpa Pass	8310'	montane forest and woodland	*Pseudotsuga menziesii*/*Populus tremuloides*
Hatch Pond	7650'	montane grassland	Grass spp./*Artemisia nova*
Dixie National Forest			
Crawford Canyon	8320'	montane forest and woodland	*Populus tremuloides*/*Abies concolor*
Blubber Creek	7940'	montane low shrubland	*Artemisia nova*/*Abies concolor*
Yankee Meadow	8300'	montane low shrubland	*Artemisia nova*/Grass spp./*Populus tremuloides*
Leeds Creek	5500'	submontane tall shrubland	*Quercus gambelii*/*Amelanchier utahensis*
Blue Spruce	7800'	montane forest and woodland	*Pinus ponderosa*/*Salix* spp.
Tantalus Flat	6500'	submontane tall shrubland	*Tamarix ramosissima*/*Salix* spp./*Pinus edulis*
Fishlake National Forest			
Burnt Flat	8750'	subalpine low shrubland	*Artemisia nova*/*Populus tremuloides*
Forshea	8860'	subalpine low shrubland	*Artemisia nova*/*Populus tremuloides*
7-Mile	9300'	subalpine low shrubland	*Artemisia nova*/*Salix* spp./*Populus tremuloides*
Eldridge Hollow	8150'	montane tall shrubland	*Artemisia tridentata*/*Populus tremuloides*
Pahvant	5538'	submontane forest and woodland	*Pinus edulis*/*Juniperus osteosperma*
Beaver Canyon	8475'	montane forest and woodland	*Salix* spp./*Pseudotsuga menziesii*/*Abies lasiocarpa*
Big Flat[a]	9022'	montane forest and woodland	Grass spp./*Abies lasiocarpa*

Appendix B. *Concluded.*

Site	Elevation	SSRFR formation	Characteristic species
Manti-LaSal National Forest			
Lake Hill	7801'	montane forest and woodland	*Populus tremuloides*
Elk Ridge	8320'	montane grassland	Grass spp./*Populus tremuloides*
Huntington Canyon	5928'	montane forest and woodland	Grass spp./*Pseudotsuga menziesii*
Warner Lake	9200'	montane forest and woodland	Grass spp./*Picea engelmannii*/*Populus tremuloides*
Deer Springs	7700'	submontane tall shrubland	*Quercus gambelii*/Grass spp.
Medicine Lake[a]	9800'	subalpine grassland	Grass spp./*Picea engelmannii* /*Populus tremuloides*
Reddick Canyon	6360'	montane forest and woodland	*Acer negundo*/Grass spp.

[a] Moved from the preceding location due to dry conditions.

Comparison of Techniques for Monitoring Riparian Birds in Grand Canyon National Park

David L. Felley[1]
Mark K. Sogge

National Biological Service
Colorado Plateau Research Station
P.O. Box 5614
Northern Arizona University
Flagstaff, Arizona 86011

Abstract. The construction of Glen Canyon Dam has had profound effects on the ecology of the riparian habitat of the Colorado River in Grand Canyon National Park. Future changes in water management will continue to affect this environment and long-term monitoring is needed to assess associated changes in riparian resources. We compared the results of point count surveys to walking surveys in these riparian habitats to test their usefulness for monitoring avian populations. Similar numbers of species were detected on walking and point count surveys. Our results show that 5-min point counts are as reliable as walking surveys for detecting species occupying a site. Abundance estimates from point counts and walking surveys were highly correlated ($r^2 = 0.98$). Both point count surveys and walking surveys were effective at generating species lists and providing an index of abundance for birds using riparian habitats in the canyon. However, because the point count survey strictly controls survey effort and reduces observer variability, it is a more appropriate technique to monitor long-term trends in species composition and abundance for many species of riparian-breeding birds in the Grand Canyon.

Key words: Avian monitoring, Colorado River, point counts.

In recent years, much attention has been focused on the conservation and management of southwestern riparian habitats for several important reasons. First, though they cover only a small percentage of the landscape, they provide habitat for a disproportionately large amount of the Southwest's wildlife. For example, 51% of the region's breeding bird species are closely associated with riparian habitats (Johnson et al. 1977). Second, these areas are heavily affected by human influences including livestock grazing, urban development, and water management (Knopf et al. 1988). The riparian habitat of the Colorado River in Grand Canyon National Park is one of the largest riparian corridors in the Southwest under the management of a conservation-oriented agency, the National Park Service (Anderson and Ruffner 1988). For these reasons, this area is of special importance for conserving wildlife in the arid Southwest.

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[1] Present address: 415 East 25th Street, Cheyenne, Wyoming 82001.

Management of Glen Canyon Dam has had profound effects on this riparian environment. Vegetation that was limited by annual flooding before the dam to a band high above the current average river stage is referred to as old-high-water-zone (OHWZ) vegetation, while vegetation that has become established since closure of the dam below the OHWZ is referred to as the new-high-water-zone (NHWZ) vegetation. The OHWZ vegetation consists mainly of mesquite (*Prosopis glandulosa*), acacia (*Acacia greggii*), and hackberry (*Celtis reticulata*). The NHWZ vegetation is dominated by salt cedar (*Tamarix chinensis*), seepwillow (*Baccharis salicifolia*), and coyote willow (Salix exigua) (Turner and Karpiscak 1980). The addition of the NHWZ vegetation has greatly increased available avian habitat, altering the riparian breeding bird community by increasing both bird abundance and species richness (Brown et al. 1987:106–117).

Changes in both the NHWZ and OHWZ vegetation will continue for many years, due to changes in water management and the dynamics of plant populations. The OHWZ is slowly dying off and moving down slope as successful reproduction of mesquite and acacia shifts closer to the river (Anderson and Ruffner 1988). The NHWZ has changed under the interim flow regime begun in 1991 (Stevens and Ayers 1994), and will probably continue changing as seral processes take place even if water management remains consistent.

The effects these changes have on the bird species using the riparian habitat will be difficult to understand without quantitative data from long-term monitoring. In the past, walking surveys were used to monitor breeding birds in the Grand Canyon (Brown and Johnson 1985, Brown 1988). We found this method to be fairly accurate (Sogge et al. 1994) in the relatively small patches of vegetation in the Grand Canyon. However, it is labor intensive and lacks strict methodology (straight-line transects, constant travel speed, etc.) to control observer variability or maintain constant survey effort (Emlen 1971). The point count survey has become a generally accepted method of avian monitoring, and has some advantages over walking surveys. By revisiting permanent sites every year and observing a designated area for a specified amount of time, point count surveys control survey effort, minimize observer bias, and collect a sample adequate for statistical analyses of population trends (Hutto et al. 1986, Ralph et al. 1993).

As part of a comprehensive avian monitoring program, we compared the results of point count surveys and walking surveys. Our purpose was to evaluate the utility of point counts for long-term avian monitoring in the Grand Canyon and learn the relationships between the two techniques. Our objectives were to: (1) compare the species lists produced by the two methods, (2) compare species-abundance estimates of the two methods, and (3) compare the reliability of each method to detect a species known to occur at a site.

Methods

We conducted point counts and walking surveys at 11 sites, each a discrete patch of riparian vegetation, between Lee's Ferry and Diamond Creek on the Colorado River in 1995 (Table 1). Sites varied in size from 1.3–7.4 ha. Point counts and walking surveys were conducted once per month at each site, March–June 1995. On each visit to a site, a walking survey was conducted on one morning and a point count survey was conducted on another. For statistical analyses, walking and point count surveys were paired by site and visit. Walking surveys consisted of one observer walking slowly through the riparian habitat, recording species and numbers of all birds observed during the survey (Brown 1988, Sogge et al. 1994). The survey was considered complete when all parts of the site had been visited. Survey length was constant for each visit to a site. Point count survey methods generally follow the recommendations of Ralph et al. (1993), consisting of repeated 5-min counts from fixed locations. A 50-m radius was used to separate bird detections into two classes– detections within 50 m (50-m point count), and detections within or beyond 50 m (unbounded point count). We located points systematically, 125 to 150 m apart, roughly paralleling the river. We located points along the center of the strip of riparian vegetation, approximately half way between the river and the upland edge of the riparian vegetation. We surveyed as many points as would fit into each site using these criteria. Number of points varied from one to five per site, depending on area, and there were 37 points altogether. Point counts lasted for 10 mins in March and 5 mins from April–June. The total time from the start of the first point count to the end of the last in each site was recorded for comparison of survey effort with walking surveys. All surveys were conducted between one-half hour before sunrise and 10:00. Analyses involved only riparian breeding birds, excluding migrants and upland breeders.

To determine the most efficient point count duration, we calculated the accumulation of new species and new individuals in successive 2-min intervals of a 10-min count period in March (Hutto et al. 1986). We made comparisons between three methods: walking surveys, 50-m point counts, and unbounded point counts. The mean number of species detected per survey and the mean number of species in common were compared using paired *t*-tests. We compared the reliability of each method to detect a species at a site given that we knew it occupied that site during the breeding season. We defined reliability of a method as the number of sites at which a species was detected by that method divided by the total number of sites at which that species was

Table 1. Location of study sites for paired walking and point count avian surveys, Grand Canyon National Park, 1995. Location is in river mile below Lee's Ferry, river right (R) or left (L), based on Stevens (1983).

Location	Number of point count stations	Average ($\bar{x}$) walking survey duration (min)
1.0 R	2	35.7
1.6 R	3	26.0
46.0 L	7	81.0
46.7 R	4	29.8
197.2 L	3	43.5
197.6 L	1	22.7
198.0 R	3	29.8
198.2 L	3	40.2
198.3 R	2	22.3
204.1 R	4	53.0
204.5 R	5	89.8

detected by any method (including casual observations). Reliability was compared using the Wilcoxon signed-rank test. We compared the abundance estimates of each technique by summing counts from all surveys in the canyon for each technique and each species. Spearman rank-correlation was used to quantify the relationships between abundance estimates of the three methods, for the 12 most common species. All means are shown ± SE.

Results

Average numbers of new species decreased steeply from 2.4 (53% of cumulative total) in the first 2-min interval and then tapered off more gradually during successive intervals (Fig. 1). The same pattern was evident for April–June. The total number of new individuals also declined in the same manner, from 2.1 (55% of cumulative total) in the first 2 mins (Fig. 2). This led us to adopt a standard 5-min count period.

Average survey duration did not differ for walking and point count surveys (walking surveys = 45 ± 3.8 mins; point count surveys = 44 ± 4.1 mins; $t = 0.15$, 77 df, $P = 0.88$). We conducted 40 pairs of walking and point

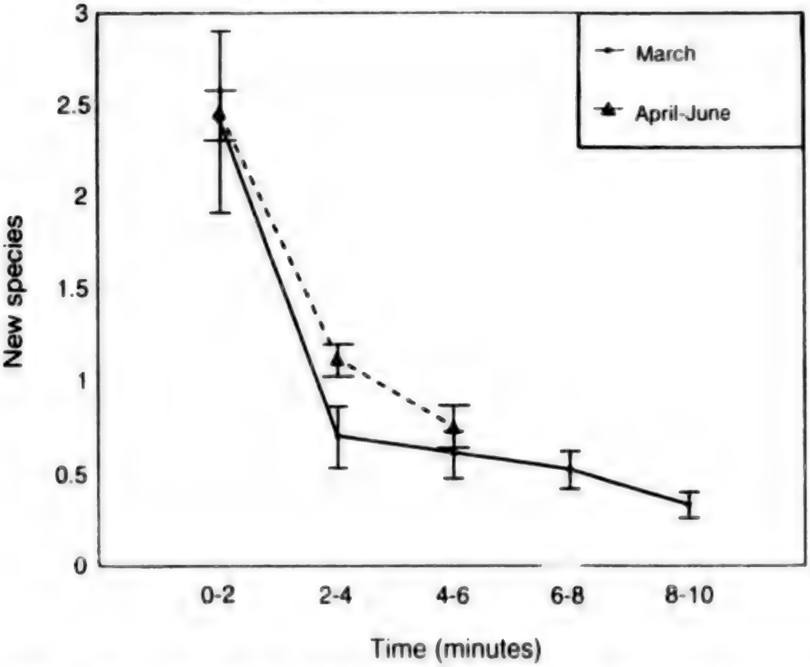

Fig. 1. Mean number of new bird species added in successive 2-minute intervals of point counts in the Grand Canyon, 1995. Error bars = S.E.

count surveys. The mean number of species detected on walking surveys (7.2 ± 0.5) was greater than on 50-m point counts (5.5 ± 0.4; t = -4.25, 39 df, P <0.001), but not on unbounded point counts (6.7 ± 0.5; t = -1.1, 39 df, P = 0.25). Not surprisingly, fewer species were detected on 50-m point counts than on unbounded point counts (t = -5.51, 39 df, P <0.001). Number of species common to paired walking and point count surveys was low; 4.3 species (60% overlap) for 50-m point counts, and 4.8 species (67% overlap) for unbounded point counts.

Of the 22 riparian breeding species present, 10 were observed on fewer than eight point counts. These included the Costa's hummingbird (*Calypte costae*), brown-crested flycatcher (*Myiarchus tyrannulus*), phainopepla (*Phainopepla nitens*), northern mockingbird (*Mimus polyglottus*), blue grosbeak (*Guiraca caerulea*), indigo bunting (*Passerina cyanea*), lazuli bunting (*P. amoena*), brown-headed cowbird (*Molothrus ater*), northern oriole (*Icterus galbula*), and summer tanager (*Piranga rubra*). Because the appearance of such rare species on a survey has more to do with chance than the effectiveness of the survey method, they were excluded from further

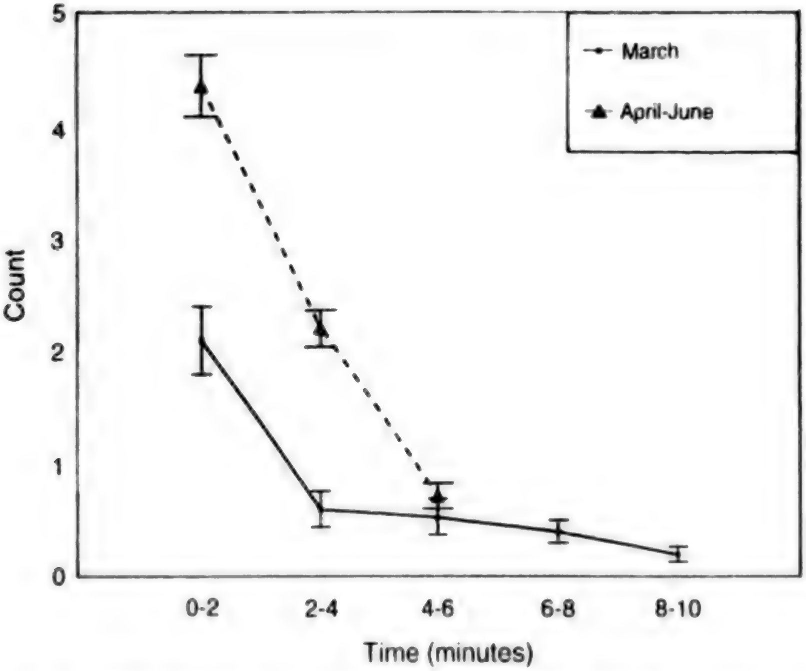

Fig. 2. Mean number of birds counted in successive 2-minute intervals of point counts in the Grand Canyon, 1995. Error bars = S.E.

comparisons. The 12 common species used for comparisons were black-chinned hummingbird (*Archilochus alexandri*), ash-throated flycatcher (*M. cinerascens*), Bewick's wren (*Thryomanes bewickii*) blue-gray gnatcatcher (*Polioptila caerulea*), Bell's vireo (*Vireo bellii*), Lucy's warbler (*Vermivora luciae*), yellow warbler (*Dendroica petechia*), yellow-breasted chat (*Icteria virens*), common yellowthroat (*Geothlypis trichas*), song sparrow (*Melospiza melodia*), house finch (*Carpodacus mexicanus*), and lesser goldfinch (*Carduelis psaltria*).

Overall walking survey reliability was 0.90, ranging from 1.0 to 0.73 for different species (Table 2). Point count survey reliability was 0.76 for 50-m point counts, ranging from 1.0 to 0.40 for different species, significantly different from walking surveys (Wilcoxon signed-rank test, Z = 2.24, P = 0.025). Point count survey reliability was 0.89 for unbounded point counts, ranging from 1.0 to 0.50. This was not significantly different from walking surveys (Z = 0.25, P = 0.80).

Table 2. Reliability of walking and point count surveys to detect bird species in Grand Canyon National Park, 1995. Reliability of a method = # of sites at which the species was detected by that method/# of sites at which the species was detected by any method.

Species	Walking	50-m radius point count	Unbounded point count
Lucy's warbler	1.0	1.0	1.0
Bell's vireo	1.0	1.0	1.0
Blue-gray gnatcatcher	0.91	1.0	1.0
Bewick's wren	0.73	0.73	1.0
House finch	1.0	0.82	1.0
Black-chinned hummingbird	0.91	0.91	0.91
Lesser goldfinch	1.0	0.86	0.86
Song sparrow	0.89	0.67	0.78
Ash-throated flycatcher	0.91	0.54	1.0
Yellow-breasted chat	0.89	0.56	0.89
Yellow warbler	0.78	0.75	0.75
Common yellowthroat	0.80	0.40	0.50
Overall	0.90	0.76	0.89

Total abundance for each species from walking surveys was highly correlated with abundance estimates from 50-m point counts ($r^2 = 0.97$, $b = 0.88$; Fig. 3) and from unbounded point counts ($r^2 = 0.94$, $b = 1.14$).

Discussion

Details of an avian monitoring program must be tailored to the geographic area under consideration and project objectives (Verner 1985, Ralph et al. 1993). These include the type of survey, duration, use of detection distances, and other variables. A primary variable of point counts is the time length of the counting period. The appropriate time length must be a compromise between efficiency (to maximize sample size) and return on effort (based on abundance of the species of interest). Hutto et al. (1986) recommended a period long enough to detect 75–80% of all species present. Ralph et al. (1993) recommend 10-min counts for general inventory surveys

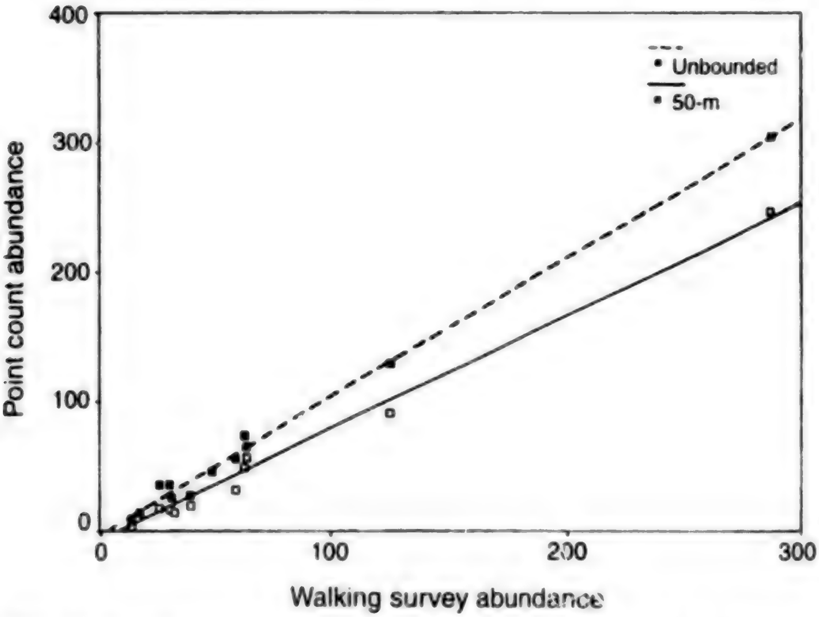

Fig. 3. Abundance estimates of birds from walking surveys in relation to abundance estimates from point count surveys of the 12 most common species, pooled for all sites surveyed in the Grand Canyon, 1995.

when distances between points are large. We detected 81% of the species observed at a site in the first 5 mins of 10-min counts. While this may not represent 81% of all species present, given the relatively low number of breeding species in the canyon's riparian environment and the great extent and remote nature of habitat in the canyon, we feel that 5-min counts represent a good compromise between completeness and efficiency. Because the time to get between points is sometimes greater than 15 mins, 10-min counts recommended by Ralph et al. (1993), would be preferable if manpower and river logistics permit.

As expected, point count detections within the 50-m fixed radius were significantly fewer than detections within and beyond 50 m. Despite this, there are several advantages to using a fixed radius. First, it helps reduce observer variability. Most competent observers will hear birds equally well within a small fixed distance, while beyond this distance individual differences cause variability to increase rapidly (Ramsey and Scott 1981). Given the small size of most habitat patches in the canyon, we believe that 50 m is appropriate for most riparian breeders.

Second, an important assumption to all survey methods is that individuals are not counted more than once. Such "double-counting" leads to positive bias in abundance estimates (Verner 1985). When the distance separating survey points is small, a small (relative to point separation) fixed detection radius can reduce the probability of counting one individual at a 2-point count station. To this end, Hutto et al. (1986) placed points 200 m apart, and Ralph et al. (1993) recommend 250 m separation. In this study, the distance between survey points, 125–150 m, increased the possibility of double-counting, especially for birds with large territories. In the small riparian patches of the canyon where counting stations may need to be closely spaced, use of a 50-m detection radius can help control this source of bias.

Differences between walking survey and point count results were probably not due to differences in survey efforts, as measured by mean survey length for the two methods. Similar numbers of species were observed during walking surveys and unbounded point counts. However, the number of species in common for the walking and point count surveys was low. This lack of agreement was largely due to observations of rare species. A statistically powerful test to compare the ability of these methods to detect rare species would require many more detections than we obtained (i.e., more visits, more points, or more surveys; Dawson 1981), justifying our exclusion of these rarer species for comparing the reliability of the methods. Also because of this limitation, monitoring population trends of rare species in the Grand Canyon will require more species-specific methods, rather than a general monitoring effort.

Excluding rare species, the reliability of the unbounded point counts and walking surveys to detect a species was similar overall, higher than the reliability of 50-m point counts. Also, certain species-specific differences were evident (Table 2). Common species with small territories, such as the Lucy's warbler and Bell's vireo were equally well detected by all three methods, because their territories were likely to fall entirely into the 50-m detection radius. The yellow-breasted chat and ash-throated flycatcher, both loud species with larger territories, were poorly detected by only the 50-m point counts. This may be because individuals within their territories were likely to be beyond the 50-m radius during the count period. The relatively quiet and rare yellow warbler was poorly detected by all methods, and probably approaches the lower limits of abundance for effective monitoring under our methodology. Finally, the common yellowthroat, a habitat specialist nesting in emergent vegetation, was especially poorly detected by both point count methods due to a methodological bias. We located point count stations halfway between the river and the upland edge of the riparian vegetation, shifting survey attention away from the river's edge where this species is usually found. Thus, survey methodology must be tailored to reflect the life history of the species to be monitored.

The preceding analyses dealt only with presence-absence data. While this may provide the most accurate way to monitor population trends, it is not as precise as abundance estimates. However, both walking and point count methods can provide only an index of abundance rather than an accurate estimate (Verner 1985). The question is whether point counts provide as good an index of abundance as walking surveys. Abundance estimates from walking and point count surveys were highly correlated. The closer *b* (slope of the relationship) is to 1.0, the closer the two variables are to a 1:1 relationship. Both point count methods were near 1:1 with the walking surveys, with 50-m point counts undercounting and unbounded point counts overcounting relative to walking surveys. The overestimate of abundance by the unbounded point counts may be due to double-counting and could be decreased by moving count stations farther apart (Hutto et al. 1986, Ralph et al. 1993).

These results show that the point count method can provide data of similar quality to walking surveys in the Grand Canyon. Both methods can detect the common riparian breeding species and give comparable estimates of abundance with the same amount of survey effort. The advantages of the point count method to standardize survey effort between years, control observer bias, and provide a sample suitable for statistical analyses, suggest that this is the better method for long-term avian monitoring in the Grand Canyon. Given the tenuous status of riparian habitats in the Southwest, of which the riparian corridor of the Colorado River in Grand Canyon National Park is a considerable fraction, monitoring riparian avian populations in the park should be given a high priority. Finally, understanding the effects of Glen Canyon Dam management on these populations can be most accurately done through such a carefully planned long-term monitoring effort.

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Characteristics of Merriam's Turkey Loafing Habitat Reused Following Silvicultural Treatment

Brian F. Wakeling

Arizona Game and Fish Department
Research Branch
2221 West Greenway Road
Phoenix, Arizona 85023

Chris J. Mehling[1]

U.S. Forest Service
Chevelon Ranger District
HC 62, Box 600
Winslow, Arizona 86047

Cheryl M. Mollohan

Arizona Game and Fish Department
Education Branch
2221 West Greenway Road
Phoenix, Arizona 85023

Abstract. We monitored known turkey loafing sites following silvicultural treatment to determine which factors seem to influence habitat reuse. Five loafing sites used by Merriam's turkey (*Meleagris gallopavo merriami*) during the summer of 1989 on the Chevelon study area were protected from subsequent silvicultural treatment. Portions of the forest stands containing the loafing sites were logged in 1990. We inspected these loafing sites annually after logging to detect reuse by turkeys. Habitat surrounding two loafing sites was reused during summer 1992. Habitat characteristics of all five loafing sites were remeasured to determine characteristics that influenced reuse. Dense canopy, dense horizontal cover, and contiguous similar habitat were characteristics of loafing sites that received reuse following logging. Loafing habitat isolated from other similar habitat was not was not reused. Mosaic timber treatments that leave areas of >25 m^2/ha basal area (BA) and avoid isolation of habitats seem to favor turkey reuse.

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[1] Present address: Arizona Game and Fish Department, Nongame Branch, 2221 West Greenway Road, Phoenix, Arizona 85023.

Key words: Forest, habitat use, loafing, logging, *Meleagris gallopavo merriami*, Merriam's turkey, timber harvest

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Loafing is a behavior in which many gallinaceous birds engage. In Merriam's turkeys, this includes resting, preening, and dusting in habitats with dense canopy (Rumble 1990, Mollohan et al. 1995). In addition to resting, because turkeys loaf more frequently during summer than winter, loafing habitat may be used to reduce thermal loading during the warmer summer months (Wakeling and Rogers 1996).

Loafing habitat is one component identified in some Merriam's turkey habitat evaluations (Hoffman et al. 1993, Mollohan et al. 1995). Validation and evaluation of research recommendations are essential because management activities are often necessarily based on observational descriptions rather than rigorously designed experiments.

Loafing sites are generally located in characteristic forest stands. Loafing sites are typified as small (0.05–0.25 ha) stands of dense pole (12–38 cm) timber immediately adjacent to drainages, >25 m^2/ha BA, containing large diameter (>30 cm) downed logs (Mollohan et al. 1995) or rock outcrops (Rumble 1990). These sites are typically interspersed within adjacent small openings used for feeding that have sharp edge contrast and escape cover (Rumble 1990, Shaw and Mollohan 1992, Mollohan et al. 1995). Loafing sites appear as dense clumps of pole timber containing large downed logs and little understory vegetation surrounded by small herbaceous openings.

We are unaware of any published information on how silvicultural treatment affected reuse of previously used loafing habitat. Our objective was to defer known loafing sites from silvicultural treatment and determine through monitoring if turkeys would reuse the loafing sites and surrounding habitats. In our monitoring efforts, the loafing sites identified within active timber sales were few in number. Consequently, we sought to identify variables potentially influencing reuse. We intend that results from our study should foster further investigations and monitoring efforts following land management activities.

Study Area and Methods

Merriam's turkey hens were captured, radio-marked (Model LB400, Telonics, Mesa, Arizona), and released at sites baited with whole oats on the Chevelon study area (CSA), Arizona (Wakeling 1991). The CSA was located approximately 65 km south of Winslow, Arizona, along the Mogollon Rim. Vegetation communities on the CSA were (1) mixed-conifer (20.1%); (2) ponderosa pine (*Pinus ponderosa*)-Gambel oak (*Quercus gambelii*) (34.9%); (3) pinyon (*Pinus edulis*)-juniper (*Juniperus* spp.) (44.4%); (4) aspen (*Populus tremuloides*) (0.4%); and (5) meadow (0.2%). A detailed description of the study area may be found in Wakeling (1997).

Visual observations were obtained from radio-marked hens to identify the exact location of loafing sites. Five loafing sites, located during summer 1989, were selected for study (Fig. 1) because they were located within the boundaries of two scheduled timber sales. The five loafing sites were located within the boundaries of the Double Cabin Timber Sale (DCTS) ($n = 2$) and the Ridge Timber Sale (RTS) ($n = 3$). Both areas were logged during 1990. The stands surrounding the two study sites in the DCTS were logged in an even-aged manner, removing all ponderosa pine trees ≥38 cm diameter at breast height (dbh). The stands surrounding the three study sites within the RTS were logged as a seed cut, removing ponderosa pine trees >23 cm dbh leave 4.6 m^2/ha basal area.

Prior to logging, habitat characteristics were measured at each study site in summer 1989. Site center was defined as the central point of the undisturbed flock when first observed. Site BA was determined by measuring the dbh of all conifers on a 0.04-ha circular plot and computing area dimensions per hectare. We examined horizontal sight distance by placing a turkey silhouette at site center and pacing away until the silhouette was completely obscured. At each site, horizontal sight distance was estimated in four directions, at right angles to each other, with the first bearing randomly determined. We calculated a mean value for each site from the four measurements. We estimated canopy density (Strickler 1959) 11.4 m from site center on each of the four bearings and averaged.

Following mensuration, each site (approximately 0.04–0.08 ha) was protected from subsequent logging in summer 1990. Following logging, loafing sites and surrounding habitat within 300 m were surveyed annually during August to detect physical sign that would indicate turkey reuse. We monitored each site during August because these sites were first used during summer, and late-summer monitoring allowed for an accumulation of physical sign that would indicate reuse. During September 1993, the center of each loafing site was relocated, bearings were identified, and loafing sites were resampled as described during initial mensuration. Because sample size was limited, we simply compared means and standard deviations for each attribute among four categories of loafing sites: between sites that were abandoned and those that were reused both pre- and post-harvest.

Results

Reuse of habitat surrounding two loafing sites within DCTS was detected during August of 1992. No reuse was detected on the remaining three sites. Because each loafing site was protected from logging, BA averaged 52 m^2/ha both before and after treatment at all sites.

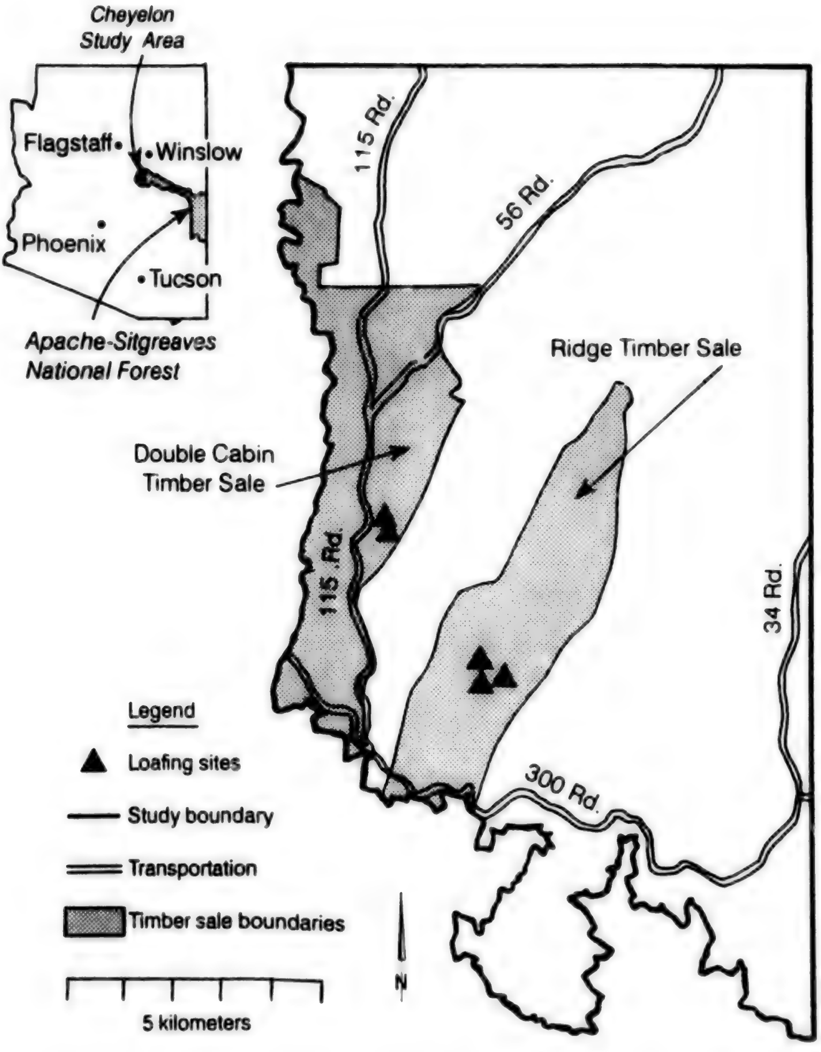

Fig. 1. Location of loafing sites within Double Cabin and Ridge Timber Sales on the Chevelon study area, Arizona.

Characteristics of all loafing sites before logging were within the range of attributes described by Mollohan et al. (1995) (Tables 1 and 2). Although all mean values following logging remained within ranges observed by Mollohan et al. (1995), those that were abandoned had mean TSD values almost two times greater than the mean identified by Mollohan et al. (1995).

Table 1. Mean, standard deviation, and range of select habitat attributes described for loafing habitat used by Merriam's turkeys (Mollohan et al. 1995).

Habitat attribute	Mean	SD	Range
Canopy density (%)	57.9	17.9	21.5–90.0
TSD (m)	22.6	7.5	9.8–40.8

Table 2. Mean and standard deviation of reused and abandoned loafing sites both before and after harvest, Chevelon study area, 1989 and 1993.

	Reused (*n* = 2)				Abandoned (*n* = 3)			
	Before		After		Before		After	
Habitat attribute	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Canopy density	84.5	5.2	79.5	12.7	65.1	16.3	65.5	11.0
TSD (m)	16.3	9.1	18.2	3.9	24.3	5.1	30.3	8.6

The abandoned sites were also greater than Mollohan et al.'s (1995) mean before logging, whereas the sites that were reused had shorter-than-average TSD values to begin with. Likewise, canopy densities were substantially lower on sites that were abandoned than those that were reused both before and after logging (Table 2). Finally, the sites in reused habitat had not been isolated from contiguous high-BA stands; those that were abandoned had been isolated by distances >12 m.

Discussion

The differences we observed between loafing sites that were abandoned following silvicultural treatment and those that continued to receive reuse are certainly not definitive. In fact, loafing behavior is not well understood. The difference in loafing frequency between seasons remains unexplained and may deal with nutritional demands or thermal loading (Wakeling and Rogers 1996). But observed differences in our study provide a starting point for future research.

Horizontal cover and canopy density seems to have influenced loafing habitat reuse. TSD was almost two times greater at abandoned loafing sites than at reused loafing sites. Mollohan et al. (1995) found mean TSD approximately equal to the reused loafing sites in our study. Although logging increased TSD at all sites in our study, those sites with substantially shorter TSDs were reused. Sites that were not reused may have been predisposed to abandonment because they had longer TSDs to start with. Dense horizontal cover may be influential in the selection of loafing habitat.

A similar relationship was apparent with canopy density, with canopy density greater on reused than on abandoned sites. However, the mean canopy density for post-harvest abandoned sites was about equal to loafing sites documented by Mollohan et al. (1995). Neither TSD or canopy density values at any loafing site in our study were outside of ranges specified as acceptable to turkeys by Mollohan et al. (1995). However, in each case where TSD was greater than and canopy density was less than the mean described by Mollohan et al. (1995), the site did not receive reuse.

Isolation (i.e., no continuous forested corridor to adjacent high-BA stands) from contiguous habitat also seemed to influence reuse of loafing habitats. Those sites that had been isolated by logging were not reused, indicating that habitat fragmentation and isolation might affect habitat reuse by turkeys. Reuse was documented in stands that retained a corridor to habitat similar in structure to that contained in the loafing site.

We believe that dense canopy, dense horizontal cover, and contiguous high-basal-area habitat are major factors influencing loafing habitat reuse by turkeys. Although our results support previous research findings (Rumble 1990, Mollohan et al. 1995), we were unable to exclude the possibility of random errors because of our small sample.

Based on our findings, we recommend further research into the ecological importance of loafing habitat. Although turkeys seem to loaf frequently during summer, the value of loafing habitat to turkeys is basically speculative and not well understood. If turkeys require loafing habitats regardless of the reasons, management of these habitats may be critical in southwestern habitats. If so, management of our forested habitats should emphasize retention of loafing habitat characteristics in silvicultural treatments. Finally, we recommend that habitat models and guidelines (e.g., Hoffman et al. 1993, Mollohan et al. 1995) be tested to determine the suitability and scope of each model. Further testing ultimately determines the quality of research recommendations in a management setting.

Acknowledgments

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Winter Movement Patterns of Merriam's Turkeys in North-central Arizona

Brian F. Wakeling

Arizona Game and Fish Department
Research Branch
2221 West Greenway Road
Phoenix, Arizona 85023

Abstract. I studied Merriam's turkey (*Meleagris gallopavo merriami*) movement patterns around roost sites in north-central Arizona during the winters of 1990–1991 through 1993–1994 to determine if distance from roost sites influenced habitat use. Knowledge of turkey movement patterns surrounding winter roosts would allow managers to predict potential adverse effects on habitat use from land management activities on winter range. I located 16 winter roost sites and 260 independent flock diurnal-use sites by visually locating radio-marked turkeys. Turkeys concentrated their diurnal use activities around roost sites, selecting areas ≤0.8 km from roost sites. Turkeys used habitat >0.8 km and ≤1.6 km from roost sites proportionate with availability and avoided habitats >1.6 km from roost sites. Land management activities ≤1.6 km from roost sites have the potential to impact wintering turkey populations. Efforts to increase suitable winter habitat for turkeys should include recruiting suitable roost sites within otherwise suitable habitat. Roost densities of ≥0.8 per km^2 seem optimal on winter turkey ranges.

Key words: Habitat selection, habitat use, *Meleagris gallopavo merriami*, roost.

Winter habitats are critical wildlife ranges. In Arizona, Merriam's turkey survival is lowest during winter, and winter habitat conditions influence mortality rates (Wakeling 1991). Timber harvesting, fuel-wood cutting, and prescribed burning are management activities that may impact turkey winter range. Natural resource managers need more information to better understand how land management activities influence winter habitat conditions.

Winter roost sites of Merriam's turkeys are typically traditional and frequently reused (Schemnitz et al. 1985). Habitat recommendations for Merriam's turkey generally suggest a minimum roost density of 0.9 per km^2 (Hoffman et al. 1993, Mollohan et al. 1995). Yet, empirical data have not been used to demonstrate that this density is adequate, nor have movements been examined around these roost sites. My objectives were to examine the influence of distance from winter roost sites to habitat use and to evaluate roost site density within habitats selected by a radio-marked population of Merriam's turkeys.

Study Area

The 860-km^2 Chevelon study area (CSA) was located on the Mogollon Rim, approximately 65 km south of Winslow, Arizona, on the Apache-Sitgreaves National Forests. Elevations ranged from 1,700 m in the northern portion to 2,430 m in the southern portion. Annual precipitation averaged 47.2 cm, with two concentrations, the first during winter storms in January through March, and the second during summer storms in July through early September (National Oceanic and Atmospheric Administration 1991).

Five cover types were present on the CSA based on U.S. Forest Service Terrestrial Ecosystem Surveys (Laing et al. 1989): (1) mixed-conifer (20.1%); (2) ponderosa pine (*Pinus ponderosa*)-Gambel oak (*Quercus gambelii*) (34.9%); (3) pinyon (*Pinus edulis*)-juniper (*Juniperus* spp.) (44.4%); (4) aspen (*Populus tremuloides*) (0.4%); and (5) meadow (0.2%). Mixed-conifer cover types were dominant above 2,340 m and extended downward along east-facing slopes and drainages. This habitat included Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), limber pine (*Pinus flexilis*), and Rocky Mountain maple (*Acer glabrum*). Ponderosa pine dominated west-facing slopes between 2,340 and 1,850 m. Below 1,850 m, the pinyon-juniper cover type was dominant, with ponderosa pine stringers along drainages. At elevations below 2,150 m, pinyon pine and alligator juniper (*Juniperus deppeana*) increased. Gambel oak occurred as a widespread codominant with ponderosa pine and in pockets in the mixed-conifer and pinyon-juniper associations.

Timber harvesting and livestock grazing were the major land uses on the CSA. Logging began in the late 1930s, and initial harvests were group or individual tree selections. Even-aged management was prevalent in the 1980s, but has been limited since 1990. Timber harvests have been conducted on 20-year stand entries, although some stands have been re-entered within 5 years. Most ponderosa pine stands on level terrain had been logged at least once; however, little logging occurred on steeper slopes in larger canyons. Cutting of fuel wood, particularly in the pinyon-juniper cover type, increased over the past two decades. Until the 1960s, sheep were the primary livestock on the CSA. Summer grazing by cattle has been the predominant livestock use on the CSA since the 1960s.

Methods

I captured turkeys during January 1 to March 31 1988–1992 with drop nets or rocket nets (Glazener et al. 1964, Bailey et al. 1980) located at sites baited with whole oats. A radio-telemetry unit (Telonics model LB 400, Mesa, Arizona) was secured on the back of each turkey with a 5-mm bungee harness.

Because I conducted trapping and capture efforts concurrently with winter movement data collection, I bisected the CSA with a north-south division closely corresponding with West Chevelon Canyon. To avoid movement biases related to artificial bait placement, I established bait sites, trapped, and radio-marked turkeys on half of the CSA. On the alternate half, I monitored movements and habitat use of previously marked birds. I annually alternated trapping and monitoring activities between sides of the CSA.

I obtained locations from radio-marked turkeys within 3.2 km of roost sites between November 15 and April 15 from 1990–1991 through 1993–1994. I located turkeys approximately twice daily, although no individual turkey or flock was located more than once daily to reduce data autocorrelation.

Locations were plotted on U.S. Geological Survey 7.5' topographic maps and Universal Transverse Mercator (UTM) coordinates recorded. Roost locations from radio-marked turkeys were also mapped and UTM coordinates recorded. A Geographical Information System (GIS) was used to plot roosts and delineate distance-class habitats of 0.8, 1.6, 2.4, and 3.2-km radii surrounding each roost site. These isometric distance-classes were used because they provided quartile classes for analysis across most turkey locations. GIS was then used to calculate the number of locations and the amount of area exclusive to each distance-class habitat. Only the area and locations ≤0.8 km from roost sites were classified as within the first distance-class, only the area and locations >0.8 and ≤1.6 km from roost sites were classified as within the second distance-class, and so on through the third and fourth distance-classes. Locations >3.2 km from roosts were excluded from analysis because the large areas and relatively few locations would result in inflated statistical probabilities.

Because of the way I located turkeys, I assumed the number of locations within each distance-class would represent the proportion of time turkeys spent within that area. I calculated the expected number of turkey locations that should have occurred within each distance-class proportionate to the area within each distance-class. I used a chi-square goodness-of-fit test to determine if turkeys used habitats of varying distances from roost sites consistent with availability. The goodness-of-fit test was appropriate because availability of distance-classes was known and not estimated from plots (Thomas and Taylor 1990). I used Bonferroni confidence intervals (Byers et al. 1984) to test for selection of individual distance-classes. Jacobs' *D* selectivity index (Jacobs 1974) was used to determine the relative degree of selection or avoidance of each distance-class habitat. I calculated the density of roost sites within those distance-class habitats that were selected and those selected and used consistent with availability to determine what density of roost sites seemed favorable to wintering turkeys.

Results

Seventy (49 F and 21 M) Merriam's turkeys were captured and radio-marked. Based on visual radio-marked turkey locations, I found 16 roosts and 341 diurnal-use sites. Only 260 locations (76.2%) were within 3.2 km of roost sites. Distance-classes around roost sites encompassed 29.4, 89.1, 150.8, and 215.2 km^2, respectively (Fig. 1).

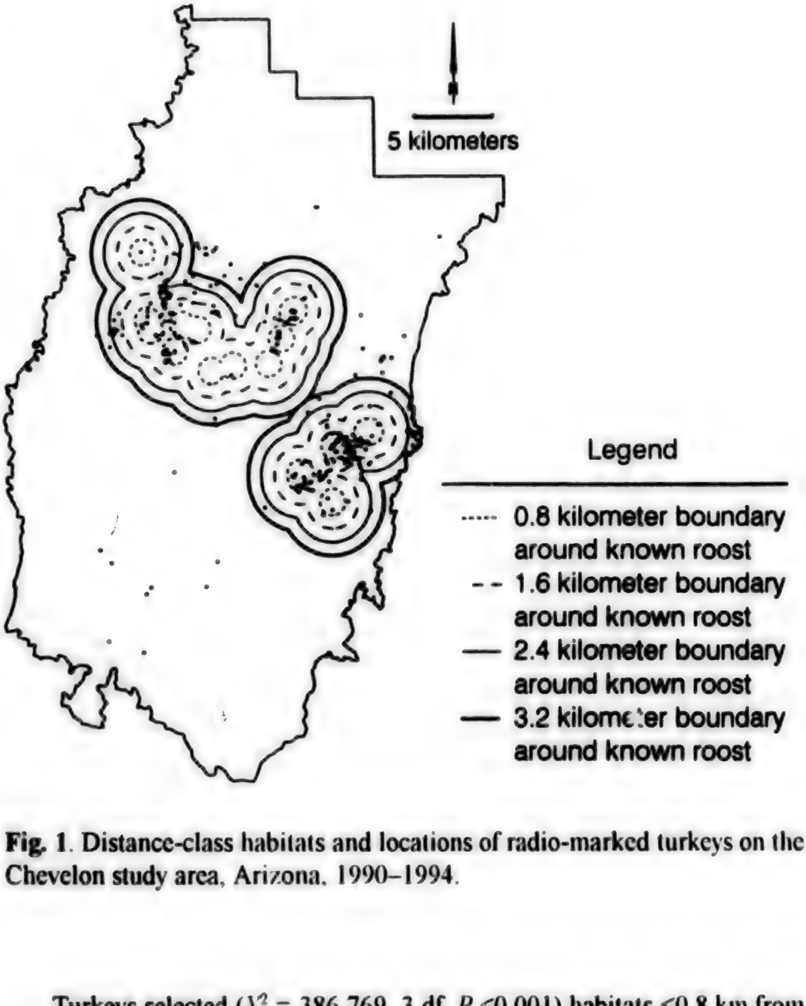
5 kilometers
Legend
0.8 kilometer boundary around known roost
1.6 kilometer boundary around known roost
2.4 kilometer boundary around known roost
3.2 kilometer boundary around known roost

Fig. 1. Distance-class habitats and locations of radio-marked turkeys on the Chevelon study area, Arizona, 1990–1994.

Turkeys selected ($\chi^2 = 386.769$, 3 df, $P < 0.001$) habitats <0.8 km from roosts for most daily activities (Table 1). Areas between 0.8 and 1.6 km from roosts were used consistent with availability. Habitats >1.6 km from roosts were used less than available for daily activities (Table 1). The density of roosts within the selected distance-class habitat (<0.8 km) from roosts was 0.8 per km^2. The density of roosts within those distance-class habitats selected and used as available (i.e., all areas <1.6 km from roosts) was 0.3 per km^2.

Table 1. Selection of concentric distance-class habitats surrounding roosts during winter by Merriam's turkey on the Chevelon study area, 1990–1994.

Distance-class (m)	Area (km^2)	Locations	Observed proportion	Expected proportion	Bonferroni confidence interval[a]	Selection[b]	Jacobs' D
0.8	29.4	118	0.469	0.131	0.387–0.551	+	0.708
1.6	68.9	86	0.343	0.307	0.265–0.421	=	
2.4	61.7	32	0.126	0.275	0.071–0.181	-	-0.449
3.2	64.5	15	0.062	0.287	0.022–0.102	-	-0.718

[a] Overall $X^2 = 386.769$, 3 df, $P < 0.001$.

[b] + denotes selection, - denotes avoidance, and = denotes use consistent with availability.

Discussion

Winter roost sites influence turkey habitat use. Turkeys used habitats close to roost sites for the bulk of their activities, avoiding those areas too far from a roost. Thus roost sites are important components to ensure widespread use of an area by turkeys. Maintenance of roost sites, therefore, is critical.

Although winter roost sites are typically traditional (Schemnitz et al. 1985), land management activities could substantially alter their use. For example, Scott and Boeker (1977) found that major alterations via timber harvest to surrounding habitats caused roost site abandonment, also resulting in abandonment of the habitat within the roost site vicinity.

Turkey winter roost sites are easily identified and can be protected from management activities. But, protecting roosts is not enough. Management activities that influence the surrounding habitat quality should also be considered when planning land management activities. Limiting land management activities that are detrimental to winter feeding habitat (Rumble and Anderson 1993, Wakeling and Rogers 1996) to only those areas >1.6 km from identified winter roost sites would favor wintering turkeys.

Roost availability would influence habitat use of large areas by turkeys. Habitats that seem otherwise suitable may simply be too far from roosting habitat. Maintaining existing roosts is important. More uniform use of habitat may be increased by recruiting suitable timber stands for potential roost sites. In one instance, the range of Rio Grande turkeys (*M. g. intermedia*) was expanded with the addition of suitable artificial roost structures (Kothmann and Litton 1975). The same effect should occur by recruiting roost sites in Merriam's turkey habitat.

Winter roost densities are critical for turkey populations. Turkeys are more dependent on fewer roost sites during winter than summer (Shaw and Mollohan 1992, Hoffman et al. 1993). Although turkeys displayed an array of affinity to roost sites in my study, they generally used a given site 10–30 days. Changes in roost site use seemed to be influenced by disturbance and food availability. Most flocks in my study used >4 roost sites per winter. Suggested roost densities of 0.9 per km^2 (Phillips 1982, Hoffman et al. 1993, Mollohan et al. 1995) may provide a lower threshold for maintaining stable turkey populations in winter habitats of the Southwest. Winter roost densities <0.3 per km^2 are probably insufficient to support wintering turkey populations.

Winter roost sites should be identified and protected from timber harvest at densities >0.9 per km^2. Some roost sites may not be used every year because nearby food sources are undependable (Wakeling and Rogers 1995); these roosts will probably be reused during more favorable subsequent years and should also be protected. Known roost sites should be recorded in a GIS database. GIS covers could then be used to identify those areas with insufficient roosts. Recruitment of suitable roost sites into low density roost areas will increase turkey habitat use. Management activities that degrade winter feeding habitat should be relegated to those areas >1.6 km from known roost sites.

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Assessment of Canopy Closure Projections by the PROGNOSIS Model

Dennis D. Haywood
Brian F. Wakeling

Arizona Game and Fish Department
Research Branch
2221 West Greenway Road
Phoenix, Arizona 85023

C. Richard Miller

Arizona Game and Fish Department
Region II
3500 S. Lake Mary Road
Flagstaff, Arizona 86001

Abstract. We studied the relationship between canopy closure derived from vertical projection and stand density index (SDI) during September 1993 on the Kaibab National Forest in northern Arizona to test predictions from the PROGNOSIS model. Management recommendations for wildlife species within southwestern ponderosa pine (*Pinus ponderosa*) forests frequently include desired canopy closures. Canopy closure estimates can be expensive to obtain beyond information collected during forest stand exams. Hence, foresters have developed models to predict canopy closure from existing data. PROGNOSIS is a model that predicts canopy closure based on SDI; the model has not been validated in Arizona. We sampled 230 random plots across 10,000 ha to develop a data set for testing. The relationship between SDI and canopy closure explained less than 50% of the variation within the data set, and PROGNOSIS consistently overestimated canopy closure when compared with estimates from vertical projection. By placing 95% confidence limits around the observed relationship between SDI and field measurements of canopy closure, we found PROGNOSIS estimates of canopy closure consistently outside the upper bounds of the relationship. PROGNOSIS should not be used in its current form to estimate canopy closure for wildlife habitat evaluations.

Key words: Habitat evaluation, habitat model, SDI, stand density index, wildlife.

Numerous authors have discussed the relationship between variations in forest structure and the relative quality of that structure as it pertains to wildlife habitat (Leopold 1949. Thomas et al. 1979, Hoover and Willis 1987). One important component of forest stand structure is crown closure. Species such as elk (*Cervus elaphus*) (Thomas et al. 1979, Brown 1991), northern goshawk (*Accipiter gentilis atricapillus*) (Kennedy 1989, Austin 1991), Merriam's turkey (*Meleagris gallopavo merriami*) (Mollohan et al. 1995), tassel-eared squirrels (*Sciurus aberti*) (Patton and Vahle 1986), and black bear (*Ursus americana*) (LeCount and Yarchin 1990) seemingly include variations in canopy closure in their selection of habitat for various behaviors. Thus, canopy closure has been established as a measure of habitat quality for many species.

Management recommendations frequently use canopy closure as a criteria for desired habitat structure (Reynolds et al. 1992, Hoffman et al. 1993). Both the U.S. Forest Service (Reynolds et al. 1992) and the Arizona Game and Fish Department (Arizona Game and Fish Department 1993) assessed proposed timber harvest effects using the timber growth and yield model PROGNOSIS (Wykoff et al. 1982). One of the outputs of this model is predictions of forest canopy closure based on stand exam data. Arizona Game and Fish Department (1993) used the model to evaluate effects of managing ponderosa pine forests in Arizona at varying tree densities, expressed in terms of Stand Density Index (SDI, Reineke 1933, McTague and Patton 1989). PROGNOSIS predicted that an SDI of 140 would yield 40% canopy closure. However, the relationship between SDI and canopy closure as predicted by PROGNOSIS has not been validated in Arizona.

The absence of this validation raised questions as to the accuracy of canopy closure predictions and reliability of subsequent applications. In addition to this concern, SDI was developed for even-aged forests and is frequently applied to forest stands that are not. Further, PROGNOSIS allows canopy closure estimates to exceed 100%, a value it then uses to provide a crown competition factor. This assumption is also often ignored in practice.

Our study was designed to evaluate the accuracy of the PROGNOSIS model in predicting canopy closure from SDI values while ignoring some underlying assumptions, as it is often used in practice. Our objectives were to (1) determine the relationship between SDI and canopy closure and (2) compare measured values with those predicted by PROGNOSIS.

Study Area

Our study was conducted on the North Kaibab Ranger District of the Kaibab National Forest, northern Arizona, in stands that had not been harvested for ≥ 10 years. Common forest trees on the area included ponderosa pine, Douglas-fir (*Pseudostuga menziesii*), white fir (*Abies concolor*), aspen (*Populus tremuloides*), and Gambel oak (*Quercus gambelii*).

Methods

Vegetation Sampling

We sampled 230 randomly located 0.04-ha circular plots. We computer-generated random Universal Transverse Mercator (UTM) coordinates to locate initial sampling points, then paced a computer-generated random distance (<100 m) on a random compass bearing to locate plot centers.

Each plot was classified by dominant trees on the sample plot. Stands with oak trees growing within ponderosa pine were considered ponderosa pine-Gambel oak type. Stands with ≥2 conifer species were considered mixed-conifer type. Those composed completely by ponderosa pine or aspen were so noted.

Canopy closure was determined by vertical projection from 20 points within each 0.04-ha plot (Johansson 1985). These 20 points were placed along a line following a randomly determined bearing, and on a second line at 90° from the first bearing (10 points on each line). Sample point placement was such that concentric rings through points equidistant from site center encompassed approximately the same area (i.e., first points were 4 m from site center and a concentric ring on plot center encompassed 50.24 m^2, second points were 5.7 m from site center and encompassed 102.02 m^2, third points were 6.8 m and encompassed 145.19 m^2, fourth points were 7.9 m from site center and encompassed 195.97 m^2, and fifth points were 8.9 m from site center and encompassed 248.72 m^2).

We read vertical projection at each point using a custom-fabricated, gimbal-suspended sighting periscope, 2.5 cm in diameter and 30.5 cm in length, with crosshairs constructed at its upper end. A mirror was mounted at the bottom of the tube to allow the observer to see the crosshair intersection while the tube was vertical. Each vertical projection reading was recorded as either under canopy or not, and what type of vegetation formed the canopy. The crosshairs had to be covered by vegetation in order to be recorded as a hit.

We measured the diameter at breast height (dbh) with a Biltmore stick for all trees on the plot >8.9 cm dbh. Each conifer tree measured on the plot was classified into one of four size classes (Table 1). A plot was then classified into one of four vegetation structural stage (VSS) classes (classes 3–6) by determining which size class yielded the greatest SDI value (Reynolds et al. 1992).

Data Analysis

Canopy closure was regressed on SDI across all dominant tree types collectively and within dominant tree type and structural stage. SDI values

Table 1. Range of tree diameters used to classify forest stands into vegetation structural stage classes.

Class lower limit (cm)	Class upper limit (cm)	VSS class
12.7	<30.5	3
30.5	<45.8	4
45.8	<61.0	5
61.0	none	6

were determined separately for all conifers, and all trees combined. SDI was calculated according to Reincke (1933) and McTague and Patton (1989) as:

$$SDI = 10n\left(\frac{\sqrt{1/n \sum_{i=1}^{n} d_i^2}}{10}\right)^{1.605}$$

where d_i represents dbh of the ith tree on the sample plot, and n represents the number of trees occurring on the plot. SDI values were calculated for each size class for each plot. Each plot was placed into VSS categories based on the dominant SDI value.

Canopy closure was computed as the percent of the 20 vertical projections in which foliage was present. Canopy closure was calculated for each dominant tree type and across all dominant tree types.

Canopy closure was also predicted for each plot according to PROGNOSIS. Logarithmic regression equations are used by PROGNOSIS to predict individual tree crown width from species, dbh, height, and crown length of trees ≥8.9 cm dbh (Moeur 1981, 1985). Height and crown length are estimated from dbh and basal area of the plot (Wykoff et al. 1982). Coefficients used in the equations were derived for the Idaho variant of ponderosa pine. We used the following equations from Wykoff et al. (1982) to predict canopy closure for each plot:

where: D = diameter at breast height
H = tree height
CL = crown length

BA = basal area
CW = crown width
CA = crown area
PA = plot area
CC = canopy closure, then

$$H = e^{4.6024 - [11.4693 / (D + 1)]} + 4.5$$

$$CL = 4.35671 + 0.84714 (D) + 0.32549 (H) - 0.03802 (BA)$$

$$\ln CW = 1.62365 + 1.08137 \ln D - 0.68098 \ln H + 0.29786 \ln CL$$

$$CW = e^{\frac{1}{2}(0.04898)} \text{ (antilog ln CW)}$$

$$CA = \pi \, (CW/2)^2$$

where *n* represents the number of trees on a plot. This canopy closure estimate was regressed on conifer SDI and canopy closure measured on the plots.

$$CC = \frac{\sum_{i=1}^{n} CA_i}{PA}$$

Results

A total of 230 plots were sampled across 10,000 ha. Samples were distributed in similar proportion across VSS classes 3–6, ranging from 20% to 33% of all observations (Table 2).

Table 2. Distribution of sample plots by vegetation structural stage on the North Kaibab Ranger District, Arizona, 1993.

VSS category	Frequency	Percent
3	50	21.7
4	46	20.0
5	58	25.2
6	76	33.1
Total	230	100.0

Regression analysis of SDI and canopy closure were conducted for the total data set and for several subsets (Table 3). All regression relations resulting from the analyses were significant ($P \leq 0.001$), indicating that the slopes of the lines differed from zero. The coefficient of simple determination (r^2) for the regressions ranged between 0.15 and 0.46 (Table 3), indicating that a relatively weak relationship existed between SDI and canopy closure. Despite a high degree of variability, SDI values related to canopy closure (Fig. 1).

Considering a 95% confidence interval around the regression line, both upper and lower confidence interval lines yielded meaningful results (Table 4). The strongest relationships were obtained for plots in the ponderosa pine vegetation type. The regression equation resulting from conifer canopy closure (canopy made up of only conifer leaves and limbs) regressed on conifer SDI (SDI calculated using only coniferous trees) yielded an r^2 of 0.46 (Fig. 1). This regression predicts that an SDI of 191 is needed to provide a mean conifer canopy closure of 40% in ponderosa pine. Total canopy closure (all canopy regardless of tree species) regressed on total SDI (all trees) yielded an r^2 of 0.39 for the ponderosa pine vegetation type. This regression predicts that an SDI of 176 is needed to provide a mean total (ponderosa pine) canopy closure of 40%.

SDI values required to yield 40% canopy closures were comparable across most subsets of the data. An r^2 of 0.34 and 0.24 resulted from regressions of conifer canopy closure and total canopy closure, respectively, on conifer SDI across all vegetation types. These regressions predict that SDIs of 182 for conifer canopy and 151 for total canopy are needed to produce a mean of 40% canopy closure. Conifer canopy closure regressed on conifer SDI in the mixed conifer vegetation type, with post-treatment plots excluded, yielded $r^2 = 0.30$ and 0.20 for total canopy closure regressed on total SDI. The mixed-conifer regressions predicted that SDIs of 148 for conifer canopy and 101 for total canopy were needed to provide a mean 40% canopy closure in mixed-conifer habitats.

PROGNOSIS estimates of canopy closure were weakly related, in a pairwise fashion, to canopy closure values measured at sample plots. PROGNOSIS estimates, regressed on measured canopy closure values, yielded an $r^2 = 0.14$ ($P = 0.001$), and a high degree of scatter. However, PROGNOSIS estimates regressed on conifer SDI (ponderosa pine plots only, Fig. 2) yielded a weak relationship ($r^2 = 0.40$, $P < 0.00001$). Still, a general trend can be seen in that increasing SDI results in increasing canopy closure estimates from PROGNOSIS. Both relationships between PROGNOSIS estimates and measured canopy closures demonstrated a high degree of variability when compared with SDI.

The algorithms utilized by PROGNOSIS yielded slightly higher canopy closure values in comparison to vertical projection measurements. This observation can be seen in the slopes of the canopy closure-SDI regressions (Figs. 1 and 2). Canopy closure estimates from PROGNOSIS ranged from 0

Table 3. Regression coefficients, significance level, and confidence intervals of measured canopy closure regressed on stand density index, North Kaibab Ranger District, Arizona, 1993.

Data set[a]	Variables							
	Predictor[b]	Response[c]	n	r^2	P	β_0	β_1	95% confidence interval on β_1
All data	TSDI	TCC	231	0.24	<0.0001	18.9	0.14	0.11–0.18
All data	TCSDI	CCC	231	0.34	<0.0001	12.7	0.16	0.13–0.18
All data	TCSDI	TCC	231	0.16	<0.0001	23.4	0.12	0.08–0.15
Ponderosa pine	TSDI	TCC	101	0.39	<0.0001	11.9	0.16	0.12–0.20
Ponderosa pine	TCSDI	CCC	101	0.46	<0.0001	8.5	0.17	0.13–0.20
Ponderosa pine	TCSDI	TCC	101	0.34	<0.0001	13.7	0.15	0.11–0.19
Mixed conifer	TSDI	TCC	83	0.20	<0.0001	26.1	0.14	0.08–0.20
Mixed conifer	TCSDI	CCC	83	0.30	<0.0001	16.0	0.16	0.11–0.22
Mixed conifer	TCSDI	TCC	83	0.15	0.0003	30.4	0.12	0.06–0.19

[a] All data includes all vegetation types, treated and untreated plots, both ponderosa pine and mixed conifer include only untreated plots in the respective vegetation type.

[b] TSDI is total SDI with all trees ≥12.5 cm dbh, regardless of tree species. TCSDI is SDI for conifer trees ≥1.5 cm dbh.

[c] TCC is total canopy closure regardless of tree species. CCC is canopy closure of conifers only.

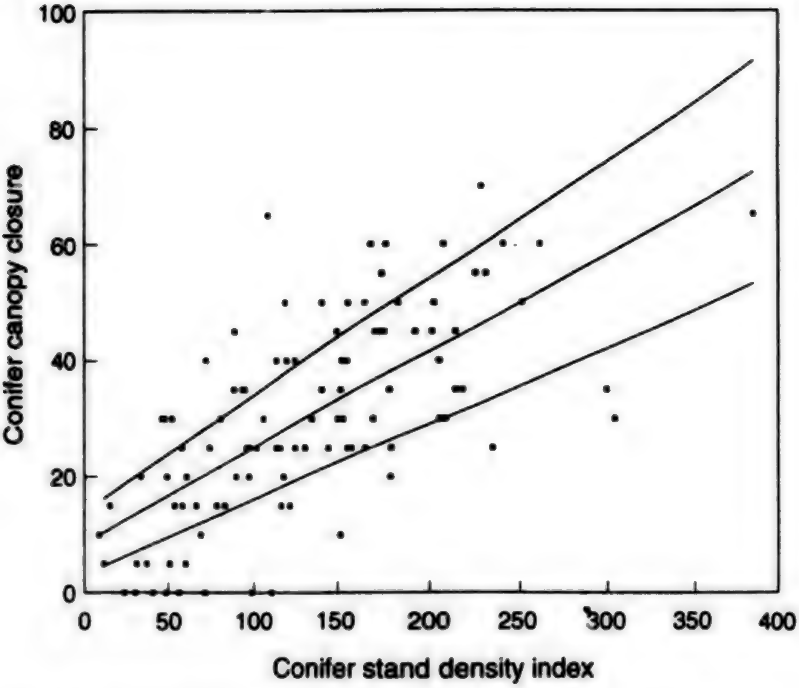

Fig. 1. Regression of measured conifer canopy closure on measured conifer stand density index, using only ponderosa pine plots (r^2 = 0.046, P = <0.0001), North Kaibab Ranger District, Arizona, 1993. Outer lines are 95% confidence limits around the regression line.

to >300%. These canopy closure estimates >100% were reassigned a maximum value of 100% for the regression mentioned above. When not so truncated the regression (estimated canopy closure on SDI) yielded an even steeper slope (β = 0.559) and a higher coefficient of determination (r^2 = 0.51, P <0.00001, Fig. 3).

We also observed a trend for higher canopy closure predicted by PROGNOSIS at the stand level than was observed at individual measured plots. In a recent PROGNOSIS simulation of forest conditions on our study area, Arizona Game and Fish Department (1993) reported canopy closures for various SDI values. We plotted these canopy closure values against SDI, and compared the resulting distribution with the observed canopy closure-SDI regression for ponderosa pine (Fig. 4). Most canopy closure estimates fell outside of the 95% regression confidence interval. The slope of the PROGNOSIS estimate trend was similar to the observed ponderosa pine

Table 4. Stand density index values needed to provide specified levels of canopy closure based on field data collected on the North Kaibab Ranger District, Arizona, 1993.

Data set[a]	Predictor[b]	Response[c]	Canopy closure (%)	Predicted SDI	95% confidence limits Lower	95% confidence limits Upper
All data	TSDI	TCC	40	151	88	239
			60	293	228	374
All data	TCSDI	CCC	40	182	129	242
			60	296	263	364
All data	TCSDI	TCC	40	138	111	208
			60	305	244	458
Ponderosa pine	TSDI	TCC	40	176	110	288
			60	301	241	401
Ponderosa pine	TCSDI	CCC	40	191	131	286
			60	303	258	396
Ponderosa pine	TCSDI	TCC	40	175	138	239
			60	309	243	421
Mixed conifer	TSDI	TCC	40	101	21	310
			60	242	170	424
Mixed conifer	TCSDI	CCC	40	148	75	293
			60	275	200	400
Mixed conifer	TCSDI	TCC	40	80	51	160

[a] All data includes all vegetation types, treated and untreated plots, both ponderosa pine and conifer include only untreated plots in the respective vegetation type.

[b] TSDI is total SDI with all trees >12.5 cm dbh regardless of tree species. TCSDI is SDI for conifer trees >12.5 cm dbh.

[c] TCC is total canopy closure regardless of tree species. CCC is canopy closure of conifers only.

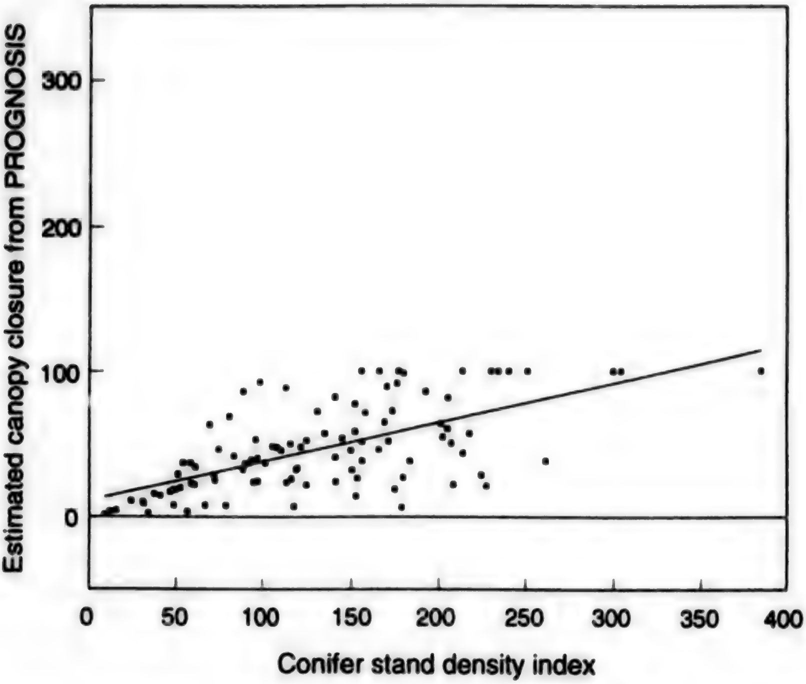

Fig. 2. Regression of conifer canopy closure estimated from PROGNOSIS equations and truncated to 100% on measured conifer stand density index, using only ponderosa pine plots ($r^2 = 0.40$, $P < 0.0001$), North Kaibab Ranger District, 1993.

relationship in our study. However the constant differed, such that lower SDI values yielded higher canopy closure estimates.

Discussion

General trends in canopy closure predictions by the PROGNOSIS model were supported by our results. However, we found an apparent upward bias in that PROGNOSIS yielded higher canopy closure estimates than we observed in the field. Data collected for any one stratum during this investigation were highly variable, indicating that factors other than SDI influence canopy closure. Uneven-aged stands increase the variability in the output from PROGNOSIS because it was designed for even-aged stands. Nevertheless, we believe that a relationship exists and that SDI can be used to manage for canopy closure if confidence interval bounds are used conservatively to predict canopy closure.

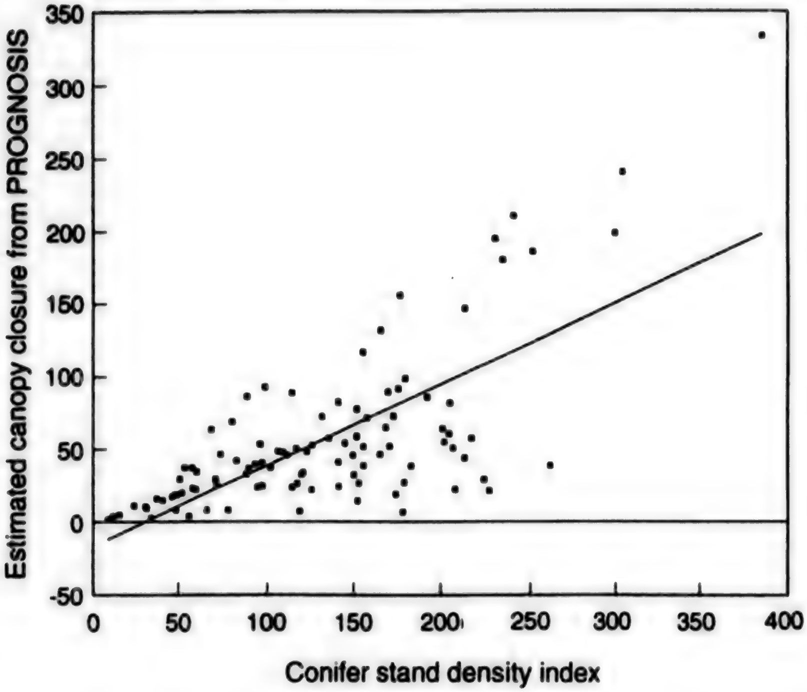

Fig. 3. Regression of conifer canopy closure estimated from PROGNOSIS equations (not truncated) on measured conifer stand density index, using only ponderosa pine plots ($r^2 = 0.51$, $P < 0.00001$), North Kaibab Ranger District, 1993.

A bias in PROGNOSIS predictions is understandable in consideration of the algorithms used to calculate canopy closure. Canopy width (and subsequently area) of a sample of individual trees is predicted, ultimately, from dbh and basal area. Basal area may be determined to represent an entire stand, and as such, applied to the computation of canopy width of each tree. We were unable to evaluate the effect of this averaging on canopy closure estimates.

Canopy closure is estimated by summing the predicted canopy area of each tree in the plot and dividing the sum by the plot area. This method cannot account for tree overlap without further site specific research and appropriate modification of coefficients. Thus, canopy closures may exceed 100%, and are by definition, biased at that point where trees begin to overlap, or canopy extends beyond the plot boundary. Additionally, we cannot evaluate the effect that aggregating tree characteristic data across plots may have on

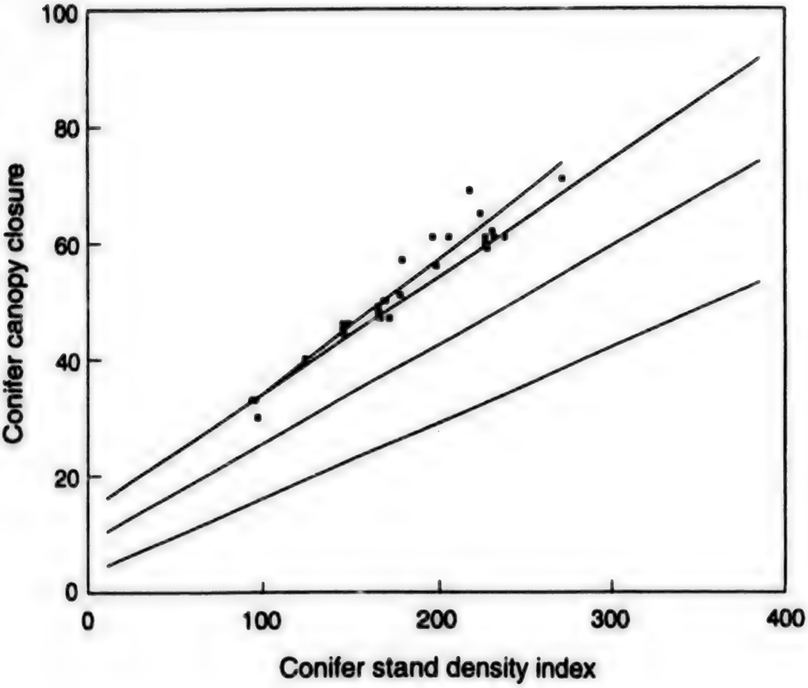

Fig. 4. Regression of conifer canopy closures, reported by Arizona Game and Fish Department (1993), estimated from PROGNOSIS equations on conifer stand density index values (short line with points) from our study area. The longer regression line and 95% confidence limits from Fig. 1 are presented for comparison.

canopy closure predictions. However, computation of one canopy closure statistic for a large stand may ignore a skewed frequency distribution of canopy areas, and as an arithmetic mean, may be biased upward by the presence of a few outliers.

A major assumption of the PROGNOSIS model is that the crown area of all trees are circular, and the total area of that circle provides cover. While the assumption may be appropriate for modeling tree growth and interaction patterns, it does not portray an accurate view of forest stand characteristics in nature. This assumption, by definition, overestimates canopy closure. Data from this study indicate that the PROGNOSIS model predictions lie at the upper edge of our observations, overestimating canopy closure for a given SDI.

Our data suggest that nearly all groups of trees sampled will meet the desired canopy closure of 40% if that stand is managed to the highest SDI in the confidence interval. Canopy closure predictions by PROGNOSIS, in its present form, should not be used to evaluate wildlife habitat. Such values will ensure that most tree groups will possess canopy closure values less than the standard described by Reynolds et al. (1992).

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Dendrochronological Analysis of Goodding Willows in Grand Canyon National Park

Joy Nystrom Mast

Department of Geography and Public Planning
Northern Arizona University
Campus Box 15016
Flagstaff, Arizona 86011

Gwendolyn Waring

School of Forestry
Northern Arizona University
Campus Box 15018
Flagstaff, Arizona 86011

Abstract. In Grand Canyon National Park, dendroecological information on Goodding willow (*Salix gooddingii*) provided an estimate of the age structure of the population and the growth rate patterns. Goodding willow, a dominant riparian tree species before the construction of Glen Canyon dam, currently is at risk due to water flow regulation destroying habitat and competition with tamarisk (*Tamarix chinensis*). Lab analyses of annual rings revealed periods of growth suppression and release. The four chronologies (upper river, mid-river, lower river, and a control site) were created to help to examine climatic influence and river regulation impacts on willow growth. The age structure analyses showed a lack of Goodding willow recruitment at the upstream site of Lees Ferry and midstream site of Cardenas Creek. It appeared that the altered flood regime caused by Glen Canyon dam, as well as possibly the increase of tamarisk invaders, have adversely affected willow recruitment along the Colorado River up to the Lake Mead area. In contrast, classic J-shaped curves existed for the downstream site of Pearce Ferry near Lake Mead and the control side stream site of Diamond Creek, representing stable or expanding populations. The dendrochronological results of this study demonstrated impacts of Glen Canyon Dam flow regulation on the Goodding willow establishment and growth rate. Specifically, data showed the importance of flood events like the 1983 record post-dam flood to establishment of new stands of Goodding willows.

Key words: Demography, flood control, Glen Canyon Dam, size structure, tree rings.

Along the Colorado River within Grand Canyon National Park, Goodding willow (*Salix gooddingii*) is the only large willow found below

Glen Canyon Dam (Turner and Karpiscak 1980). Goodding willow, a dominant riparian tree species prior to the construction of Glen Canyon dam in 1963, currently is at risk due to water flow regulation destroying habitat and competition with tamarisk (*Tamarix chinensis*). Little recruitment and high mortality are evident in upstream populations that are now comprised mainly of decadent individuals. Goodding willow recruitment and establishment are dependent on periodic floods (Reichenbacher 1984). Although rare for the majority of the park, Goodding willows are abundant on exposed benches of sediments near Lake Mead. Yet even this population may be in danger from fluctuating lake levels.

Glen Canyon Dam has strongly influenced the Colorado River and its riparian vegetation since dam completion in 1963. Located 15 river miles upstream from Lees Ferry, the dam regulates the river's flow through a daily cycle based on electricity demands with little seasonal variation (Howard and Dolan 1981). Consequences of this river regulation include lower mean annual maximum flows (Fig. 1), flood control, higher median flows, colder and less variable river temperatures, sediment trapping, and beach erosion (Thomas et. al. 1960, Carothers and Dolan 1982, Stevens 1983).

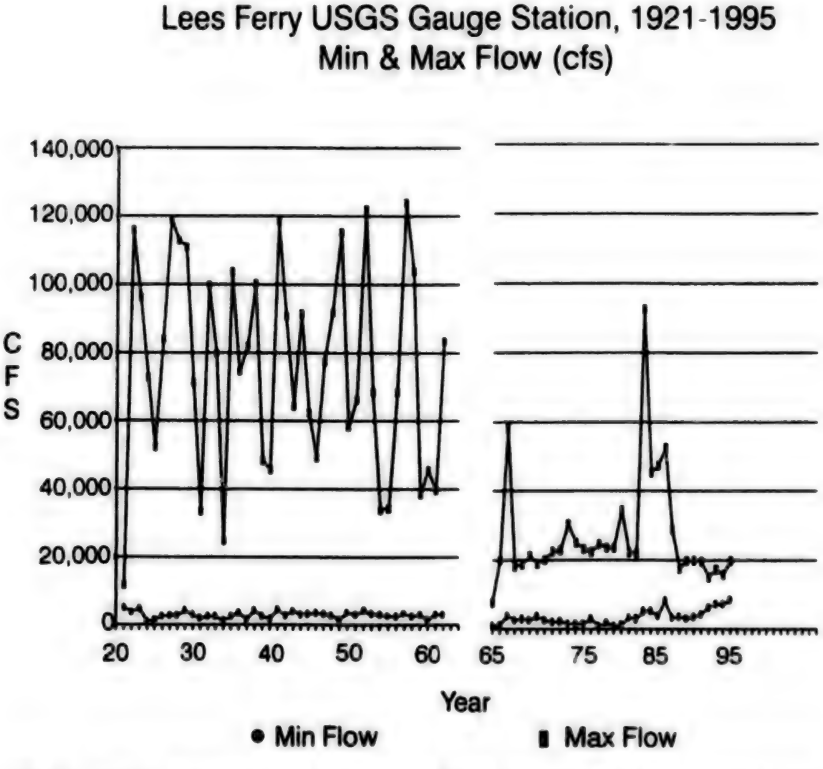

Fig. 1. Yearly minimum and maximum flows, in cubic feet per second (cfs) for the Colorado River, recorded at Lees Ferry, Arizona.

These changes due to river regulation provide a stable habitat for riparian vegetation (Turner and Karpiscak 1980). Currently, the riparian vegetation communities consist of old high water and new high water bands, reflecting the flood lines before and after Glen Canyon Dam construction. For the majority of Grand Canyon National Park, old high water vegetation consists of mesquite (*Prosopis glandulosa*) and catclaw (*Acacia greggii*) while new high water zone includes tamarisk, mesquite, seep-willows (*Baccharis* spp.) and coyote willow (*Salix exigua*) (Stevens 1983).

Before dam construction, frequent high level flooding limited the amount of vegetation along the Colorado River in Grand Canyon National Park (Clover and Jotter 1944). Following the construction of the dam in 1963, riparian vegetation expanded and diversified (Carothers and Aitchison 1976, Purcherelli 1986, Stevens and Waring 1988). Although many species have increased their distribution since dam construction, Goodding willow appears not to be recruiting in most of the Grand Canyon National Park. Possible reasons for the lack of willow seedlings are the decline in sediment quality and expanding competing vegetation. However, Goodding willows are becoming established at sites in Upper Lake Mead, possibly due to ample bare sediments.

Dendrochronological information can provide an estimate of the health of the willow population. Tree ring patterns reflect climatic influences and river regulation impacts on establishment and growth. Demographic field studies also help in analyses of willow responses to flood flows (Stromberg et al. 1991). In this study, we compared dendrochronological evidence of willow establishment and growth rate to flow records. Of particular interest was the impact of Glen Canyon Dam after 1963 and the record post-dam flood in 1983 (recorded at 92,600 cubic feet per second, or 2,622 cubic meters per second).

Age, size, and growth rate data on willows throughout the river corridor in the Grand Canyon National Park provided for a more complete understanding of the fate of this species. This research was part of an extensive demographic study of Goodding willows in the Grand Canyon. The larger study seeks to detect broad scale shifts in willow distribution from the upper to lower Grand Canyon region.

Study Site

The Colorado River extends for 277 miles (447 km) through Grand Canyon National Park in Arizona. Park boundaries officially start at Lees Ferry (river mile 0) and end below Grand Wash Cliffs (at the beginning of Lake Mead, river mile 277; Fig. 2). In this stretch, the Colorado River ranges from 76 to 300 feet (23 to 91 m) in width, with an average depth of 35 feet (10.6 m), and descends from an elevation of 3,116 feet to 1,200 feet (949 m to 365 m) (Stevens 1983). Reflecting elevational differences, the mean annual

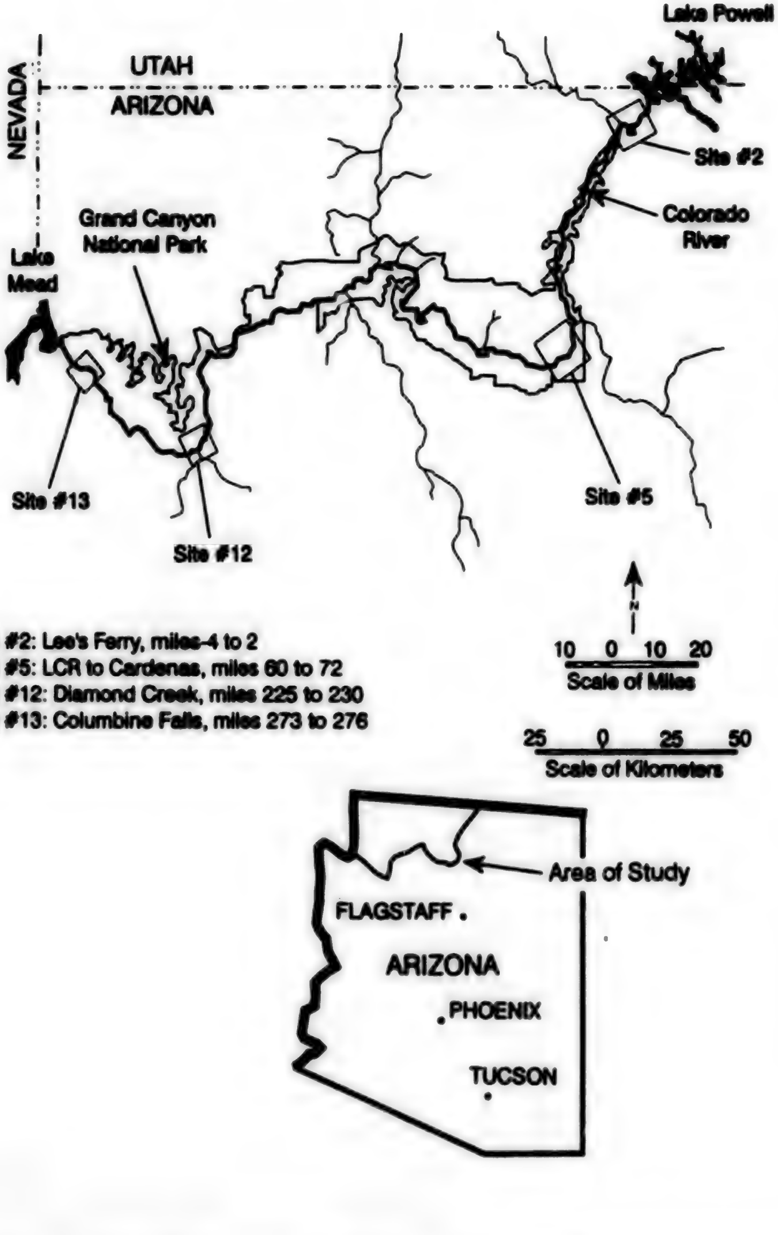
Lake Powell
UTAH
ARIZONA
NEVADA
Site #2
Colorado River
Grand Canyon National Park
Lake Mead
Site #13
Site #12
Site #5
N
Site #2: Lee's Ferry, miles-4 to 2
Site #5: LCR to Cardenas, miles 60 to 72
Site #12: Diamond Creek, miles 225 to 230
Site #13: Columbine Falls, miles 273 to 276
10 0 10 20
Scale of Miles
25 0 25 50
Scale of Kilometers
Area of Study
FLAGSTAFF
ARIZONA
PHOENIX
TUCSON

Fig. 2. Study sites for Goodding willow research in Grand Canyon National Park, Arizona.

air temperature varies from 63°F (17.2 °C) at Lees Ferry to 66°F (18.9°C) at Lake Mead, while the annual precipitation is highly variable with summer monsoons from mid-July to September (Sellers and Hill 1974). Mean yearly precipitation is 5.8 inches (14.7 cm) upstream at Lees Ferry, 8.4 inches (21.3 cm) midstream at Phantom Ranch, and 4.6 inches (11.7 cm) downstream at Lake Mead (Stevens 1983).

This study included Goodding willow samples from the entire stretch of the Colorado River through Grand Canyon National Park. Three main regions contain populations of willows: (1) Lees Ferry (river mile 0), (2) Cardenas Creek (around river mile 71), and (3) above Pearce Ferry (river mile 267-274; Fig. 2). To include willows not affected by Colorado River regulation influences, we also studied a side canyon at Diamond Creek (river mile 226). In addition, we examined scattered individual willows accessible by boat at river mile 209 and 220 and at Granite, Unkar, and Nevilles Rapids.

Methods

Field Methods

We collected dendroecological information from 290 Goodding willows, which we cored approximately 10 cm above the ground, and measured diameters at ground height (dgh). Tree condition data included stem count, number of dead stems, and beaver or flood damage. At each field site, numbered tags were attached to cored willows to designate permanent plots, while marked aerial photographs were used to denote plot boundaries. Permanent plots are important for long-term research on willow regeneration, establishment, and mortality along the Colorado River in Grand Canyon National Park.

Laboratory Methods

Following the procedures of Stokes and Smiley (1968), successively finer grades of sandpaper were used to reveal annual rings in mounted cores. We used binocular microscopes for counting tree rings to indicate tree age at coring height. Ring-width chronologies were helpful for examining influences of climate, physical disturbance, and river flow on tree growth. A computer-compatible incremental measuring machine was used to assist in determining ring widths (to the nearest 0.01 mm) on 15 willows systematically selected in each of the four main sampling areas. In addition, visual cross-dating allowed for comparison with the computer cross-dating results.

The following programs were used for creating the tree-ring chronologies for each of the four main sites. First, the tree ring program COFECHA (Holmes 1983) was used to assist in locating missing rings or measurement errors in the tree-ring measurement series. Next, the program ARSTAN (Cook and Holmes 1992) was used to create tree ring chronologies by detrending and indexing the measurement series, then created a mean chronology. This study used a cubic spline fit (preserving 50% of the variance) division to compute indices, and a biweight robust mean to enhance the common signal. The detrending option of a cubic spline fit removed the ring-width variance attributed to tree growth geometry (smaller rings as tree ages due to greater tree diameter) (Fritts 1976). For each chronology, the earliest year included was based on a minimum of 5 of the 15 measured cores being represented, while the last year was always 1994.

Results and Discussion

Age Analyses

Overall, 77% of the 290 cores removed during this study contained piths (the other 23% dated to minimum age due to rotten centers). The percentage of willows with pith dates varied by site (28% of Lees Ferry, versus 83% of Cardenas Creek and 98% of Pearce Ferry). Overall age structure (all sites combined) followed a typical J-shape curve showing the majority of trees established since the dam construction in 1963 (Fig. 3). Note, however, that the largest willows yielded estimates of only a minimum age due to rotten centers (hence, they are not included in the age structure diagram).

Comparing the three river sites (Fig. 3), only the upstream site of Lees Ferry contained willows dating back to the 1930s. Of the 80 willows sampled at Lees Ferry (representing nearly 100% of the population at that location), 65% of the willows were multi-stemmed, 38% possessed one or more dead stems, 12% were completely dead, and 20% exhibited beaver damage. The vast majority of willows at this site could not be dated either because of rotten centers (60%) or because of tree death (12%). Of the willows having complete ring structure and piths at this site, a peak in establishment occurred from 1983–1986 (post-1983 flood establishment displayed in Fig. 1). The age-distribution histogram for this site indicated a lack of willow recruitment (Fig 3). Besides the influence of the dam, another explanation for this age distribution shape may be that the willow population was invaded by another species (tamarisk). Yet, since 72% of these cores lacked complete ages, size structure analyses may provide more useful summary data.

At the midstream site of Cardenas Creek, the oldest Goodding willows dated back to the 1950s. Of the 60 willows sampled, 50% were multi-stemmed, 22% had at least one dead stem (none were completely dead), and 42% showed beaver damage. At this site, 83% of the willows were dated to the pith, while only 17% had rotten centers. Establishment periods at Cardenas Creek included 1966–1968 and 1974–1976 (after an increase in

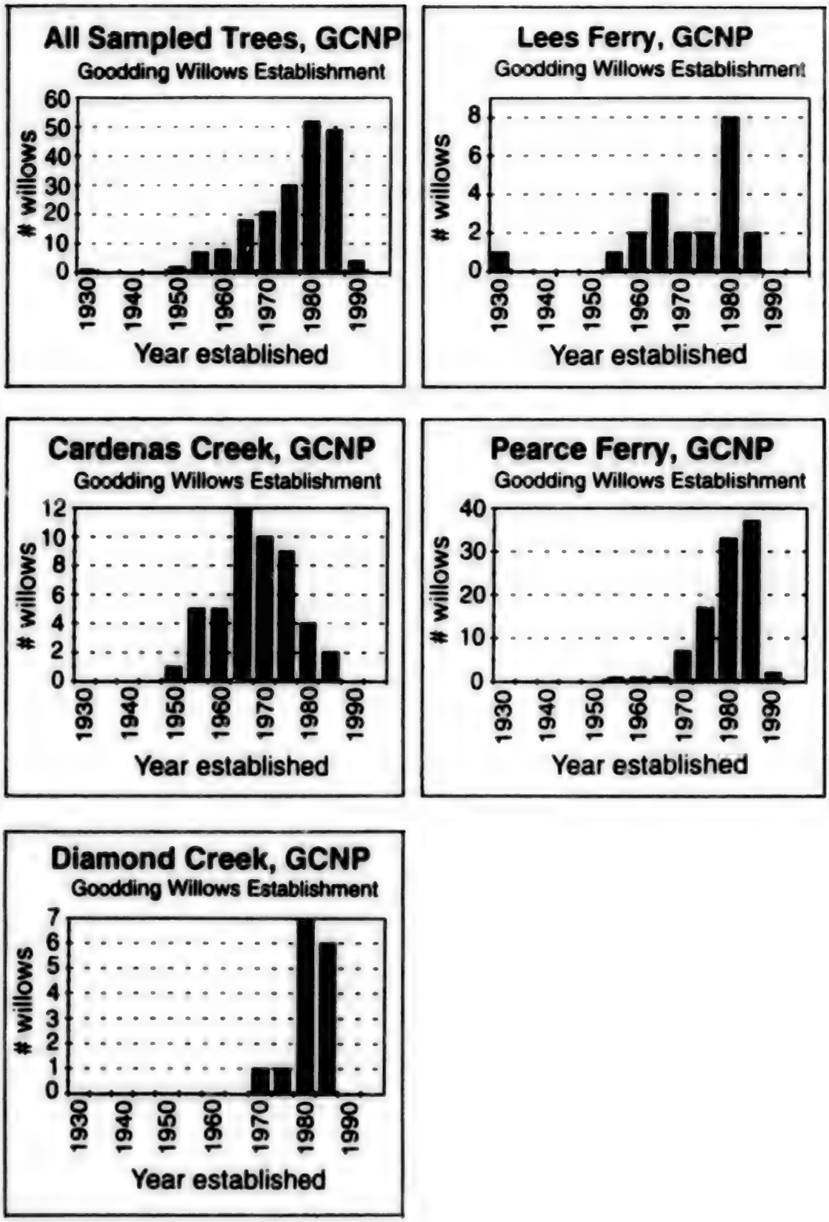

Fig. 3. Age structure analyses by site for Goodding willows, based on 5-year establishment periods, Grand Canyon National Park, Arizona, 1930–1995.

maximum flow in 1973, shown in Fig. 1). Similar to Lees Ferry, the age-distribution histogram at Cardenas Creek indicated a lack of willow recruitment (Fig. 3), possibly due to flow regulation from the dam or competition with tamarisk.

At the downstream site of Pearce Ferry only one willow dated back to 1957, while 107 of 110 willows had been established since 1972. Sixteen percent were multi-stemmed, none had dead stems, and only 6% showed beaver damage. At this site, 98% of the willows were dated to the pith, with only 2% with rotten centers. At Pearce Ferry, 58% of the dated willows established in the period 1984–1989 (following the 1983 flood). The age distribution at this site followed the classic J-shaped curve, representing a stable or expanding population (Fig. 3).

Similar to Pearce Ferry, the control side-canyon site of Diamond Creek had Goodding willows that only dated back to 1972, although two large trees (55 and 25 cm dgh) could not be completely dated. Of the 20 willow samples, 40% had multiple stems, none had dead stems, and only 5% showed beaver damage. Seventy-five percent of the Diamond Creek cores possessed piths (25% with rotten centers). Forty percent of the willows at this control site were established in 1981–1982 or 1986. Similar to Pearce Ferry, the age distribution at Diamond Creek followed the broad J-shaped curve, portraying a stable or expanding population (Fig. 3).

Size Analyses

For all sites combined, size analyses for cored Goodding willows (based on diameters at ground height) followed a typical reverse-J curve, with the majority of trees in the smaller (5–20 cm dgh) size classes (Fig. 4). The largest willow recorded, 105 cm dgh, was located as a lone tree at river mile 209 (due to rot, the core yielded only 17 rings). When analyzed by site, Lees Ferry possessed the largest average diameter willows with seven trees (11%) at 57–87 dgh. Two other size cohorts were also identified at Lees Ferry: 39 trees (63%) at 10–24 cm dgh and 14 trees (23%) at 30–49 cm dgh. One willow at Cardenas Creek reached 85 cm dgh, but the majority (78%) ranged from 10–25 cm dgh. In contrast, the largest willow in the sample area at Pearce Ferry was measured at only 33.5 cm dgh, with almost all willows (91%) between 5–19 cm dgh. Similarly, at the control site of Diamond Creek, almost all willows achieved a diameter at ground height under 20 cm, with only one large tree at 55 cm dgh.

The size class distributions (Fig. 4) supported the finding of the age-distribution histograms (Fig. 3). Both Lees Ferry and Cardenas Creek showed a lack of willows in the 0–9 cm dgh size classes, but included scattered individuals in the >40 cm dgh classes. This was interpreted as a population with little to no recruitment. Conversely, the Pearce Ferry and Diamond

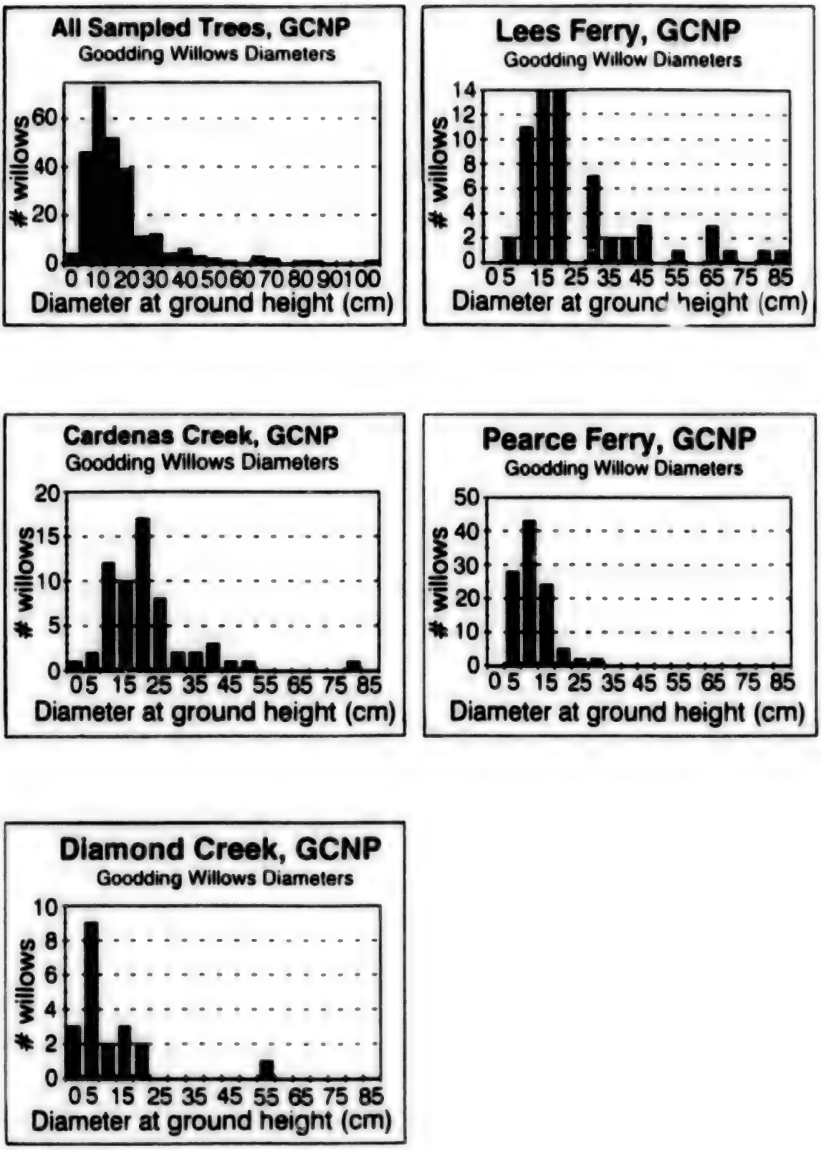

Fig. 4. Size structure analyses (diameter at ground height) by site for Goodding willows, Grand Canyon National Park, Arizona.

Creek sites displayed a classic reverse-J shaped curve with greatest numbers of willows in the smaller size classes (expected in a stable of expanding population).

Growth Trends

A comparison of master chronologies from sites along the Colorado River showed decreased growth following dam construction (Fig. 5). At Lees Ferry, significant decreased growth started in 1965, one year after dam completion. In contrast, willows farther downstream at Cardenas Creek exhibited decreased growth starting in 1970, 7 years later. The apparent delayed reactions may have resulted from the mitigating effects of the Little Colorado River that junctions with the Colorado River 9 miles upstream from Cardenas Creek. Similarly, the willows at the Pearce Ferry site displayed a marked decrease in growth starting in 1971. This may represent a delayed reaction to Glen Canyon dam, or possibly reflect fluctuating levels in Lake Mead.

From our comparison of sites along the Colorado River, Cardenas Creek's master chronology showed a significant increase in growth after the 1983 post-dam record flood (Fig. 5). These willows displayed a clear growth release starting in 1985, likely reflecting the 1983 flood and above average maximum flows in 1984–1986. The growth release peaked in 1987, but willow growth overall has remained high, possibly due to the 1983 flood that removed competing vegetation (resulting in a stand thinning release).

Diamond Creek showed potentially climate-induced growth trends. Key years of decreased growth included 1976–1977 and 1980–1982, with 2 years of increased growth in 1975 and 1978. None of the three Colorado River sites displayed significant growth changes during these periods. In turn, the Diamond Creek master chronology displayed no evidence of releases following the 1983 flood, an anticipated result since Colorado River flow fluctuations should not influence these willows.

Conclusions and Future Research

The age structure analyses showed a lack of Goodding willow recruitment at the upstream site of Lees Ferry and midstream site of Cardenas Creek. It appeared that the altered flood regime caused by Glen Canyon dam, as well as possibly the increase of tamarisk invaders, have adversely affected willow recruitment along the Colorado River up to the Lake Mead area. In contrast, classic J-shaped curves existed for Pearce Ferry near Lake Mead and the control side stream site of Diamond Creek, representing stable or expanding populations.

The dendrochronological results of this study demonstrated impacts of Glen Canyon Dam flow regulation on the Goodding willow establishment and growth rate. Specifically, data showed the importance of flood events like the

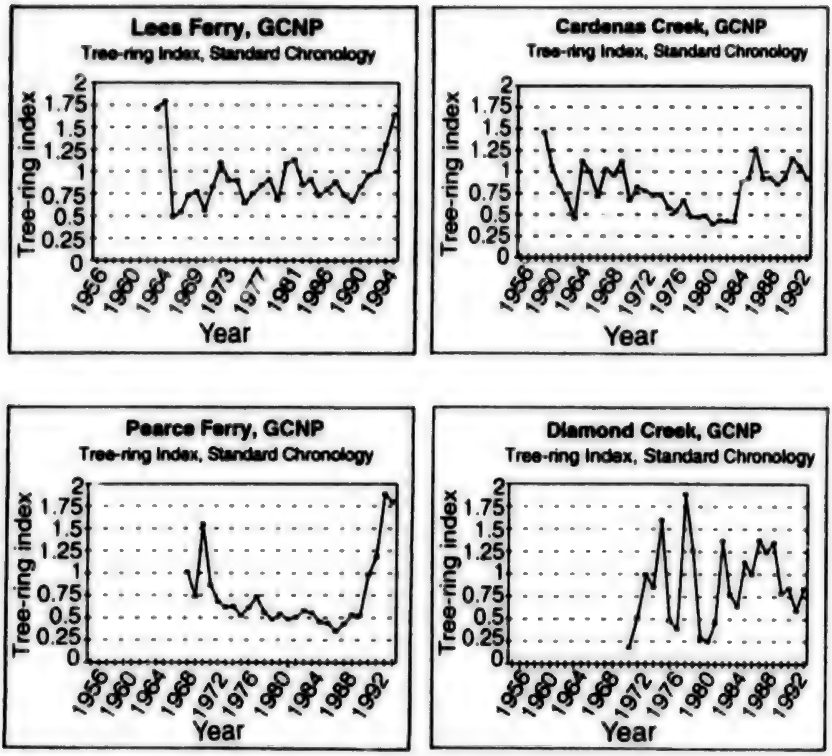

Fig. 5. Tree-ring growth records (1956–1994) for Goodding willows, displayed as standard chronologies by site, Grand Canyon National Park, Arizona.

1983 record post-dam flood to produce growth releases. Such large releases are essential to maintain populations of Goodding willow in the Grand Canyon ecosystem. The master chronology of one of the three river sites (Cardenas Creek) showed a significant increase in growth starting in 1985, likely reflecting increased sediment and nutrient availability that occurred as a result of the 1983 flood and above average maximum flows in 1984–1986. The sustained willow release may indicate that the 1983 flood caused stand thinning and reduced competition.

Our continuing demographic studies will help to detect broad scale shifts in the species distribution from the upper canyon (Lees Ferry) area to lower Grand Canyon (Pearce Ferry) region. Future studies will include analyses of willow seedling locations, willow sex ratios, impacts of beaver and rust (plant disease), effects of competition with exotic plants (especially tamarisk), and influence of soil on establishment. In addition, this study will continue to analyze dendrochronological results, comparing tree growth to lake level fluctuations in Lake Mead and flow records of the Little Colorado River and Diamond Creek. Finally, we will also be analyzing these data against the instrumental climate records to show that the growth variation observed in the cores is not caused by climatic variations but instead by alteration in river flow due to dam operations.

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After 100 Years of Forest Management: "The North Kaibab"

L. D. Garrett
M. H. Soulen

Grand Canyon Monitoring and Research Center
Flagstaff, Arizona

J. R. Ellenwood

Kaibab National Forest
Williams, Arizona

Abstract. Assessment of 100 years of forest overstory data on the North Kaibab Ranger District reveals significant changes in overstory character and structure. Evaluation of early written observations by explorers, surveyors and naturalists indicate that tree densities of the 1850s were low and the forest floor had minimal fuel loads. Recent research in restoration ecology on the district indicates pre-European settlement tree densities were originally 30–60 trees per acre. Analyses of surveys completed in 1910, 1955, 1977, and 1993, reveal that tree densities below 6" diameter at breast height (dbh) have increased from 107 trees per acre in 1910 to over 900 today. Number of trees above 6" dbh have increased from 45.3 trees per acre in 1910 to 115 in 1993. These increases have occurred with concurrent managed harvests of over 1.4 billion board feet of timber from the 1920s through 1994. Analysis of current conditions reveals 25% of the forest is potentially at high risk, and over 65% at potentially medium to high risk of ecosystem loss to insect and disease and/or wildfire. New ecosystem management guidelines, especially in regards to threatened and endangered species, could contribute to increased densities on the North Kaibab.

Key words: Ecosystem analysis, forest resource assessment, Geographic Information System, Kaibab National Forest, *Pinus ponderosa*, ponderosa pine, stand density index, tree densities.

In 1893, Congress authorized the establishment of the Grand Cañon Forest Preserve, a high plateau forest located on the north rim of the Grand Canyon in Arizona (U.S. Forest Service 1968). In 1906, President Theodore Roosevelt, a hunting enthusiast, designated the Kaibab Plateau area as the Grand Canyon Game Preserve. In 1908, the area became part of the larger Kaibab National Forest, extending south beyond Williams, Arizona. In 1919, the southern extremity of the Kaibab Plateau, which abuts the northern rim of the Grand Canyon, was made part of the Grand Canyon National Park (U.S. Forest Service 1968, Baker et al. 1988).

Today, after 100 years, the U.S. Forest Service continues to manage over 655,000 acres of shrubland, woodland, ponderosa pine, mixed conifer, and spruce-fir forests on the Kaibab Plateau. The Plateau is one of four districts on the Kaibab National Forest and is designated the North Kaibab Ranger District (NKRD) (Fig. 1).

The NKRDs first forest management treatments came at the direction of Dr. Bernard Fernow, the first Chief Forester of the Division of Forestry, then in the Department of the Interior. Dr. Fernow considered the ponderosa pine regions of Arizona to be well suited for timber production (Fernow 1897).

NKRD has passed through an ever evolving, but reasonably stable, management philosophy of the U.S. Forest Service for 100 years. It was characterized as "wise use," by Gifford Pinchot, the first Chief Forester of the U.S. Forest Service, and has since adopted concepts of multiple use management, and derivations thereof, including integrated resource management, and currently ecosystem management (West 1992).

This paper is drafted from a more comprehensive technical report (Garrett 1995), which describes U.S. Forest Service management on the Kaibab Plateau over the last 100 years and the changing management direction to both biophysical resource and socioeconomic infrastructure in the region. We address here only one aspect of ongoing assessments noted: the changing ponderosa pine overstory on the North Kaibab. Included are discussions of the dynamics of the overstory from 1893–1993, changing silvicultural practices, and probable implications of increasing tree densities. Finally, we pose questions regarding newly implemented ecosystem management guidelines and their potential implications.

Assessment Procedures

Our evaluations on the North Kaibab Ranger District is an attempt to examine several important components of the forest ecosystem. The ponderosa pine forest overstory is the most dominant resource in this forested landscape. Management of this overstory is under intense controversy, implying the need for improved knowledge of how it is changing, and the implications of these changes.

Because approaches to ecosystem management should attempt to analyze biophysical resources through time and space, we utilized a geographic information system as a tool for much of our comparative analysis. This required, in some instances, development of algorithms to compare, for example, the 1910 Kaibab forest reconnaissance (Lang and Stewart 1910), to the 1993 forest assessment (U.S. Forest Service 1994). Due to differing sampling methodologies used in several overstory surveys from 1910 and

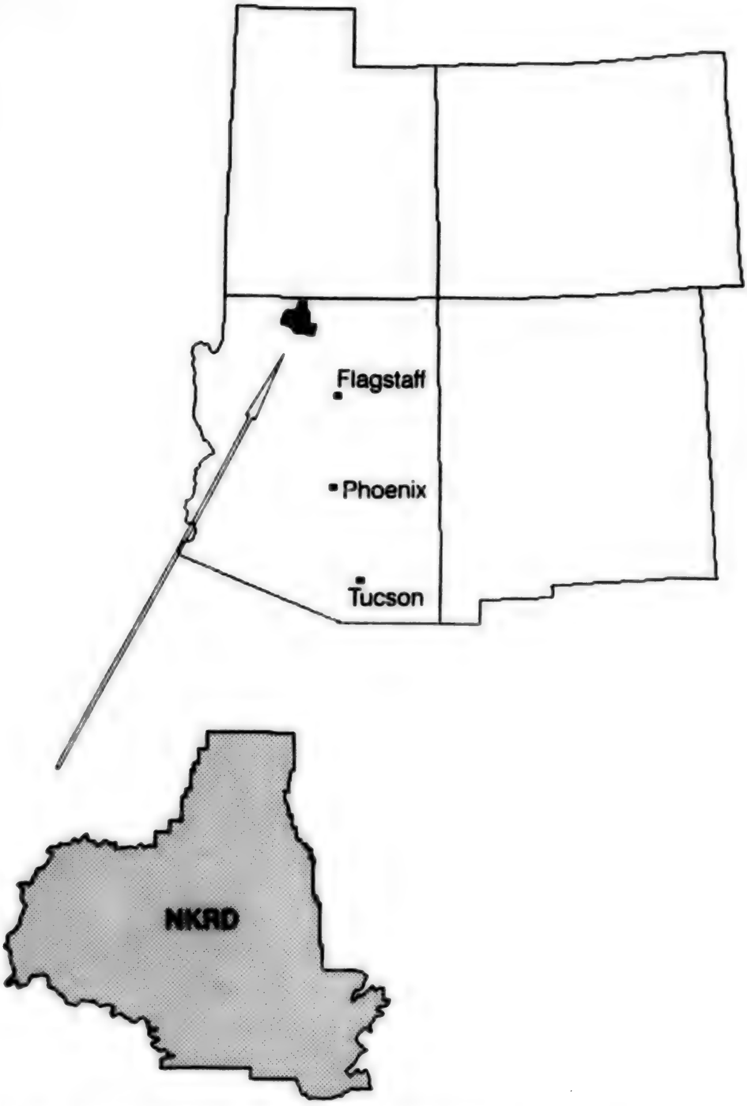

Fig. 1. The North Kaibab Ranger District (NKRD) in Arizona.

1994, derived measurements are not statistically comparable. This paper, therefore, presents descriptive comparisons of the 1910, 1955, 1977, and 1993 resource surveys, contrasting variables in the databases. Complete descriptions of original survey procedures, and procedures for conforming different databases for analysis in GIS, can be found in Garrett (1995) and Ellenwood (1994).

A Changing Forest Overstory

To evaluate a century of changes in the North Kaibab Ranger District forest overstory, we first describe the forest's general character in the pre-European settlement period of the mid–1800s. We then describe changes in the overstory through this century.

Although Native American occupation and Anglo-American visitations to Arizona's ponderosa pine forests predated the 1800s period, written observations of Arizona's ponderosa pine forests do not appear in the literature until the mid–1800s (Cooper 1960). Collectively, there are many written descriptive observations on these ponderosa pine forests during the late 1800s. The observations recorded by early naturalists and explorers are very similar, and afford valuable descriptions of the forest character and structure.

For example, in 1858, Edward Beale, a surveyor for the transcontinental railroad traveling south of the Grand Canyon recorded the following:

> "A vast forest of gigantic pines, inserted frequently with open glades, sprinkled all over with mountains, meadows, and covered with the richest grasses, was traversed by our party for many days. We came to a glorious forest of lofty pines, through which we have traveled ten miles. The country was beautifully undulating, and although we usually associate the idea of barrenness with the pine regions, that was not so in this sense; every foot being covered with the finest grass and beautiful grassy glades extending in every direction. The forest was perfectly open and unencumbered with brush wood, so that the traveling was excellent" (Beale 1858).

And in the classic "Physical Geology of the Grand Canyon Region," Dutton (1882) describes the ponderosa pine forests of the Kaibab Plateau as follows:

> "The trees are large and noble in aspect and stand widely apart, except in the highest parts of the plateau where the spruces predominate. Instead of dense thickets where we are shut in by impenetrable foliage, we can look far beyond and see the tree trunks vanishing away like an infinite colonnade. The ground is unobstructed and inviting. There is a constant succession of parks and glades, dreamy avenues of grass and flowers winding between sylvan walls, or spreading out in broad open meadows. From June until September there is a display of wild flowers which is quite beyond description" (Dutton 1882).

By the first decade of the 1900s many of the southwest forest areas had been surveyed by professional foresters. Involved with these surveys was

Theodore Woolsey (1911), who coordinated a survey for forests of Arizona and New Mexico. The survey determined average stand conditions as well as stand conditions for the most dense stands surveyed in eight southwestern national forests in the 1911 period. He also provided some of the first technical descriptions of the pre-settlement pine forests of the Southwest, as follows:

> "A true park-like stand made up of scattered groups of from 2 to 20 trees usually connected by a scattering of individuals. Openings are frequent, and very great in size within the forests. Open parks of large extent whose origin may be due to peculiar soil conditions such as hardpan, or in other cases periodic flooding" (Woolsey 1911).

The first overstory survey of the North Kaibab ponderosa pine forest ecosystem was conducted in 1910 (Lang and Stewart 1910). The 1910 survey mapped out 353,938 acres of forested land and 5,197 acres of grassland, of which 266,042 acres of forest and 4,556 acres of grassland fall within the current boundary of the Kaibab National Forest (Ellenwood 1994). Between this first decade and the fifth decade of the century, analysis of the overstory was primarily captured in working circle plans and area management plans of the forests (U.S. Forest Service 1988). At the mid-century, sampling based continuing forest inventories (CFI) were established on the North Kaibab (U.S. Forest Service 1988). These efforts were to be repeated every 10 years to identify changes in character and structure due to both natural and anthropogenic phenomena.

In the 1970s, compartment exams were implemented to quantitatively evaluate stratified stand conditions and to produce silvicultural prescriptions (U.S. Forest Service 1994). In the early 1980s, terrestrial ecosystem surveys were introduced, and in 1985 there was an interest to increase area resolution and include other resources such as understory plant diversity and forest floor conditions (U.S. Forest Service 1988). Compartment exams became stand exams, to facilitate integrated stand management (ISM). This prompted the introduction of stand level assessments referred to as stage 2 stand inventory procedures (U.S. Forest Service 1993). Information from several of these sources has been evaluated to assess overstory changes through time. We have chosen to focus on trees per acre as the descriptor of change.

Figure 2 presents a 3-picture sequence from a permanent photo point of changes in forest overstory on the Fort Valley Experimental Forest, located in the southwestern ponderosa pine type near Flagstaff, Arizona, and now under continuous study for over 75 years (1909–1990). Pictures a, b, and c contrast 75 years of change in the overstory. In 1909, less than 50 trees per acre above 6" dbh existed on the site. In 1990, over 160 trees per acre greater than 6" dbh existed in the area (Covington and Moore 1994).

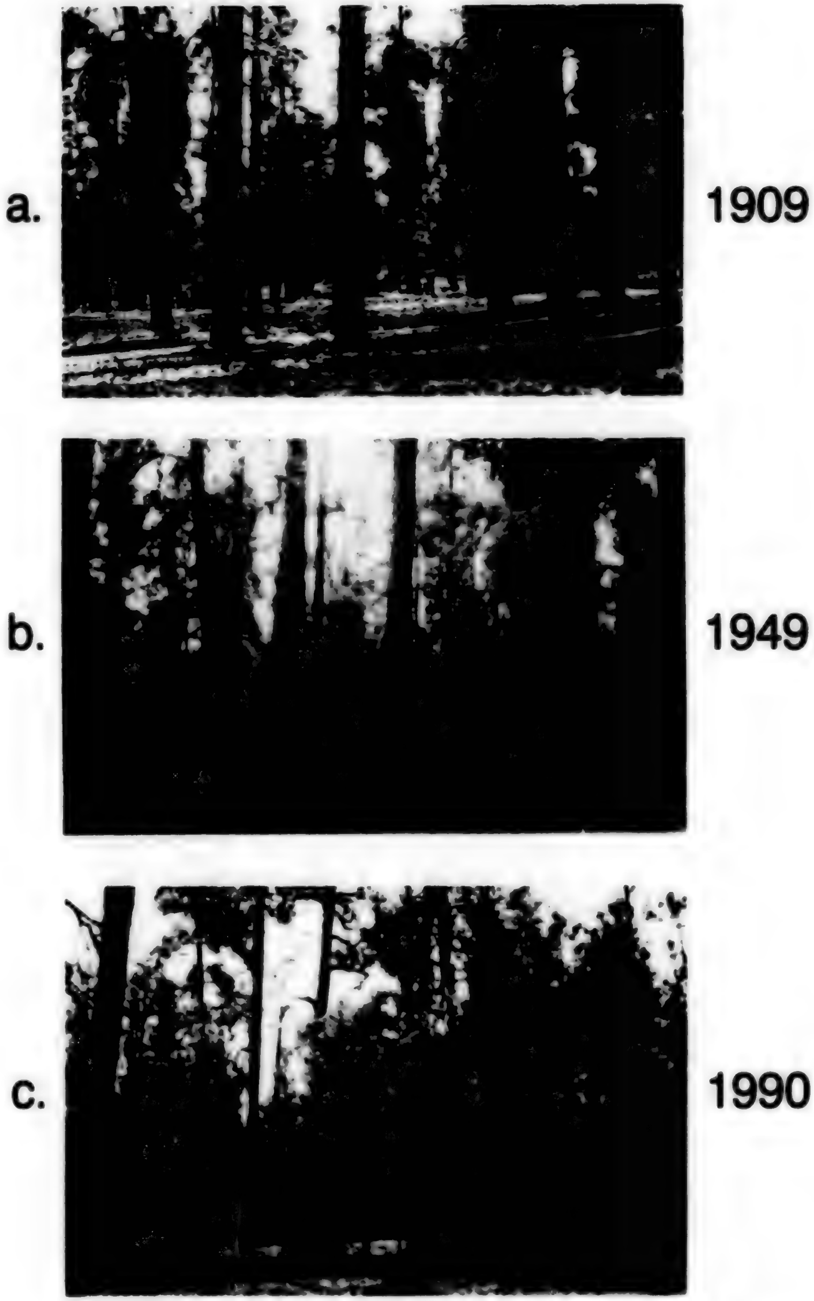

Fig. 2. Changes in forest overstory from a permanent photo point, Fort Valley Experiment Forest, Coconino National Forest, Arizona: 1909–1990.

Several forest researchers since the 1950s have evaluated changing ponderosa pine overstories of the Southwest, including Weaver (1951), Cooper (1960), White (1985), Covington and Sackett (1986), Covington and Moore (1994), and Ellenwood (1994). These studies have linked critical management actions of wildfire suppression, public land grazing, and tree harvests to current modified overstories and increasing tree densities now apparent across the entire range of this ecotype.

Restoration ecology research on the North Kaibab by Covington and Moore (1992) characterizes the presettlement forest prior to 1882 as having approximately 55.9 trees per acre. Descriptions provided in early writings, and restoration ecology research since the 1950s, can be used to characterize the pre-European settlement ponderosa pine forest as follows:

> "The southwest ponderosa pine forest overstory was most likely a fire driven ecology, with tree densities controlled by wildfire regimes moving across the landscape at 3 to 12 year intervals. This resulted in removal of most ground fuels and extensive suppression of regeneration. Resulting overstory was a mosaic of low density stands dominated by larger diameter trees located in clumps of 2 to 30 and averaging 30 to 50 trees per acre."

Overstory Inventories: 1910–1993

Figure 3 presents survey comparisons of changing character and structure of the North Kaibab's forest overstory from Lang and Stewart's first survey in 1910 through the 1993 forest assessment (U.S. Forest Service 1994). Trees per acre by diameter class are the comparative factor derived from these surveys. Trees per acre contribute to development of important measures of competition in forest overstories, including basal area and stand density index.

The comprehensive reconnaissance of the North Kaibab forest by Lang and Stewart (1910), reported the average trees per acre at 152.4 (Ellenwood 1994). The average number of trees below 6" dbh was 107 and above 6" dbh was 45.3. Most of the 6" dbh and larger trees lay between 6" and 18" dbh. Only 9.8 trees per acre were greater than 20" dbh. And, although there was a large tree component on the Kaibab Plateau, on average only 1.4 trees per acre existed over 30" dbh.

Studies have demonstrated that the mortality of ponderosa pine increases with both diameter and stand density (McTague 1990). Larger trees, normally the product of age, have greater susceptibility from such damaging agents as lightning, wind, crown fires, bark beetles, and other agents (Pearson 1950, Schubert 1974). Both Pearson (1940, 1950) and Schubert (1974) have associated higher mortality in this species with larger (greater than 28" dbh) and older trees.

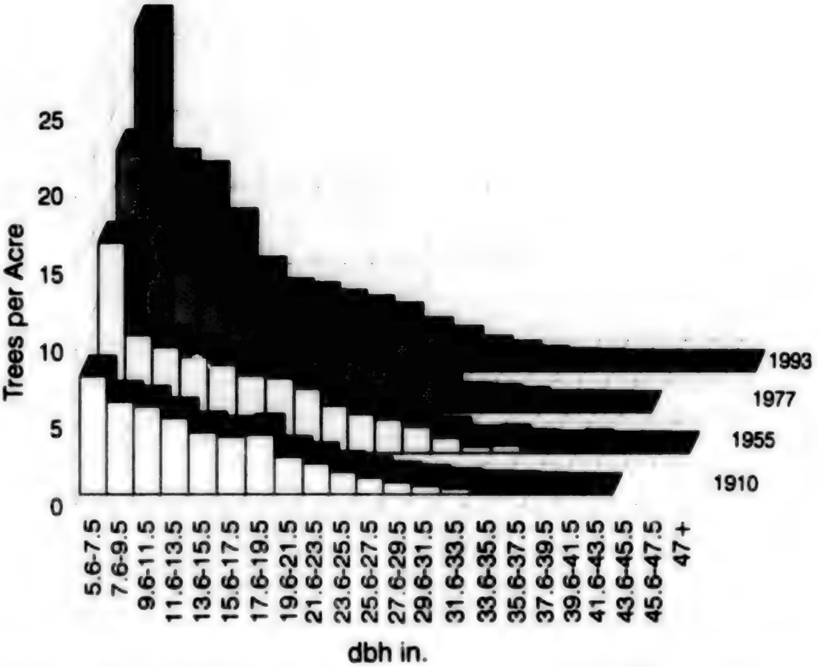

Fig. 3. Trees per acre in the North Kaibab ponderosa pine type: 1910–1993.

The fact that only 43.5 trees per acre existed above 6" dbh in 1910 lends credibility to the argument by restoration ecologists that presettlement ponderosa pine forests were dominated by approximately 30–60 trees per acre (Covington and Moore 1992). The fact that livestock grazing and wildfire suppression were introduced to the southwest forests in the 1870–1910 period, allowed four decades for recruitment of new trees in the 1 to 6" dbh classes, and movement of trees existing in the 3 to 6" dbh classes into the 6 to 8" diameter classes (U.S. Forest Service 1988). If fire had continued in these ecosystems, it is likely that many of the trees 0 to 6" dbh would not have survived. Further, even fewer trees would have grown into the 6 to 8" dbh classes, putting the total number of trees above 6" dbh at 20–35, instead of 43.5.

The 1955 continuous forest inventory (CFI) revealed that the 1910, 3 to 6" dbh trees, had grown significantly so that the average number of trees above 6" dbh was now 73 trees per acre, compared to 45.3 in 1910. Trees below 6" had also increased radically, from 107 to 422 trees per acre.

The 1977 forest survey revealed a continued expansion of the forest above 6" dbh (Fig. 2). Although recruitment into dbh classes above 6" had increased, these increases were partially offset by expanded timber stand improvement cuttings, thinnings and commercial harvests, as well as mortality in larger trees. The overall average number of trees above 6" dbh increased to 92 per acre as compared to 73 trees in 1955. The gradual movement of the 1910 6 to 12" dbh classes into higher diameter classes is apparent in Fig. 3.

Tree harvest levels increased during the 1950s and 1960s to approximately 60 million board feet per acre by the late 1970s (U.S. Forest Service 1993). These harvest levels continued until 1991 and have since declined due to increasing opposition to management activities on federal forest lands. However, in spite of these harvests, the 1993 assessment of trees per acre above 6" dbh demonstrates continued gains in the 6 to 15" and 20 to 30" dbh classes. Further, the total number of trees above 6" dbh continued to increase to an average of 115 trees per acre.

Figure 4 characterizes by diameter class the net change in trees per acre above 6" dbh between the 1910 and 1993 surveys. All size classes from 6 to 30" dbh have increased in stocking in 80 years, moving from a total of 43.5 trees per acre in 1910 to 115 trees in 1993.

Since no extensive survey of the North Kaibab area existed prior to 1850, a direct comparison of the 1993 stocking levels above 6" dbh cannot be made to pre-European settlement forest conditions. However, using Woolsey's (1911) assessments and restoration ecologists' definition of pre-European settlement forest conditions, the 1993 inventory data indicate that forest overstory densities above 6" dbh on the North Kaibab today are somewhere between 250 and 350% greater than densities in the early 1800s. Increased densities below 6" dbh also occurred. Whereas Lang and Stewart (1910) recorded an average of 107 trees below 6" dbh in 1910, 422 trees were recorded in 1955 and 943 in 1993.

Further, it is difficult to ascertain what average maximum stocking potential can be reached below 6" dbh. Examples exist on several forests where stocking below 6" dbh across stands can exceed 1,500 trees per acre (Pearson 1950, Schubert 1974, Covington and Moore 1994). Given a reoccurrence of optimal regeneration conditions as witnessed in 1919, significant increases could continue to occur in these diameter classes (Pearson 1950).

Trees above 6" dbh in diameter are also likely to increase unless more intensive management actions are taken. As noted in Fig. 4, most of this increase has occurred between 6" and 15", with additional increases occurring between 20" and 30" dbh. When the entire plateau is considered, these diameter classes now contain millions more trees than they did in 1910.

The data indicate that over the century only a slight increase has occurred on the Plateau in number of trees above 30". On some acres where more intensive harvest or high mortality has occurred there have been reductions

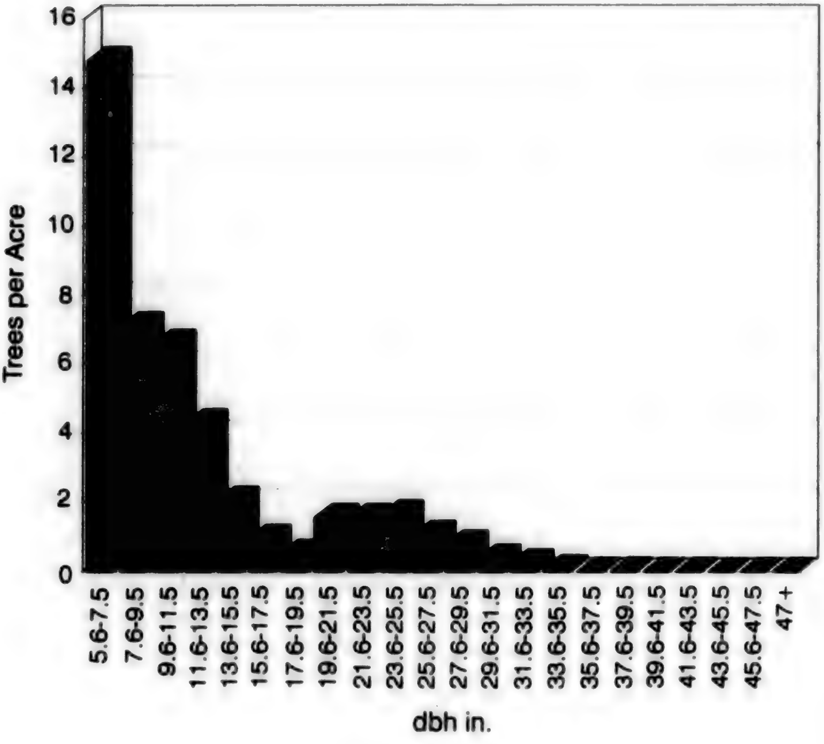

Fig. 4. North Kaibab ponderosa pine type: Net change in trees per acre. 1910–1993.

in very large trees per acre. These are obviously balanced by acreages where numbers of trees above 30" have increased due to ingrowth.

The greatest concern revealed by these comparative data is that there are greater than average increased densities continuing in diameter classes 6–15" dbh and 20–30". These trees will continue to grow, expanding both their crown and root systems. As they express greater dominance in capturing increasing levels of soil moisture, nutrients and solar insolation, they will afford a significant environmental threat to all old large trees as well as herbage production (Schubert 1974, Clary 1978, Covington and Moore 1994).

Overstory Management, Harvests and Mortality

The type of silvicultural management practiced is always diverse for different forest types and differing management objectives. The general harvest practice on the North Kaibab for the first half of this century was to remove overmature, diseased, deformed, and mistletoe trees. These individual selection removals resulted in an average of 1,500 board feet per acre being harvested, during which time the average wood volume rose from 4,000 board feet per acre to 9,600 board feet per acre across the plateau (U.S. Forest Service 1993).

Prior to 1946, removals were minimal from the North Kaibab (U.S. Forest Service 1993). There were several small mills which only impacted localized areas. In 1946, Whiting Brothers opened a small mill in Fredonia, eventually constructing a large capacity mill in 1948. After 1948, they were the principal buyer of forest products from Forest Service lands on the North Kaibab.

In the mid-1980s, ISM was implemented on the plateau, which basically focused on stand specific objectives. The timber management plan in effect at that time recommended even-aged management. Most of the ISM treatments followed even-aged regeneration prescriptions such as shelterwood and seed-tree cuts.

On seed-tree cut sites, 10 to 13 trees per acre in the 18 to 24" dbh size class were left for a seed source and site protection. Smaller trees were cut to prepare the site for new regeneration. Heavier cutting occurred in areas with severe dwarf-mistletoe infections, which often left fewer seed trees and required fill-in planting to assure adequate and timely regeneration.

From 1976 to 1993, a total of 33,661 acres of pre-commercial thinnings were conducted to reduce stocking of smaller trees (U.S. Forest Service 1993). However, this equates to only one pre-commercial thinning for each rotation of trees, which is inadequate to control increased stocking of small trees. Schubert (1974) viewed this increased stocking as contributing to increased insect and disease infestations and eventually increased losses to wildfire.

The primary disease attacking ponderosa pine on the Plateau is dwarf mistletoe. It too existed throughout the range of ponderosa pine in the presettlement period and today is one of four major causes of mortality in southwestern ponderosa pine overstories (Schubert 1974). On trees not killed, it is responsible for about 15% reduction in growth. It is more pervasive in dense stands under increased stress.

Lightning strikes and associated wildfire have always been a prominent natural mortality factor in this ecosystem. However, the type and level of risk and impact from lightning and wildfire has changed due to increased tree densities. In pre-European settlement times, lightning was the most critical agent in causing loss of old mature trees (Woolsey 1911, Pearson 1950).

Wildfire was a ground-based phenomenon placing only regeneration at risk. Current wildfires, however, are more intense due to increased densities, which provide both greater ground fuel loads and fuel ladders (Covington and Moore 1994).

Reductions to the forest overstory also result from commercial harvest of wood products. In general, under existing sustained yield policy guidelines, forest managers are to implement removals only to a level that does not inhibit the ability of the forest to provide a continued sustained flow of wood products (U.S. Forest Service 1994). Figures 5 and 6 illustrate where commercial harvest removals have occurred on the NKRD since its establishment. In total, over 1.4 billion board feet of commercial products have been removed since the early 1920s (U.S. Forest Service 1993). Figure 5 is a graphic of all areas where selection harvest treatments were applied. The dark areas represent stands that were harvested, thinned or treated from 1965 to 1984, with removals accounting for approximately 1,500 board feet per acre (U.S. Forest Service 1994).

In the mid-1980s, under new silvicultural approaches of integrated stand management and integrated resource management, shelterwood and seed tree harvests were established removing an average of 3,500 board feet per acre in treated areas (U.S. Forest Service 1994). In Fig. 6, treatments are represented by rectangular cutting units interspersed, primarily on a north/south axis in the central portion of the forest. Shelterwood harvests, applied with integrated resource management in the mid-1980s, have now changed to ecosystem management, which will utilize developed standards and guidelines for implementation. Whereas the traditional focus of multiple use and integrated resource management was on management of the forest for use, such as commodity products, services and amenity values, ecosystem management focuses not just on traditional resource uses, but also on intrinsic values of the land including biodiversity, health and sustainability.

Implementation of Ecosystem Management and Protection of Biodiversity

As noted, one focus of ecosystem management is protection and maintenance of biodiversity in an ecosystem. This includes development of standards and guidelines for activity implementation. In general, these guidelines act as constraints, both temporally and spatially on any activities that might be proposed for areas within the forest ecosystem.

Examples of standards and guidelines associated with protecting biodiversity, are those related to creating protective habitat for the sensitive northern goshawk, and endangered Mexican spotted owl. However, constraints proposed as developed guidelines could also severely impact potential restoration treatments to reduce increasing tree densities in these critical habitat areas. The total number of acres withdrawn is significant.

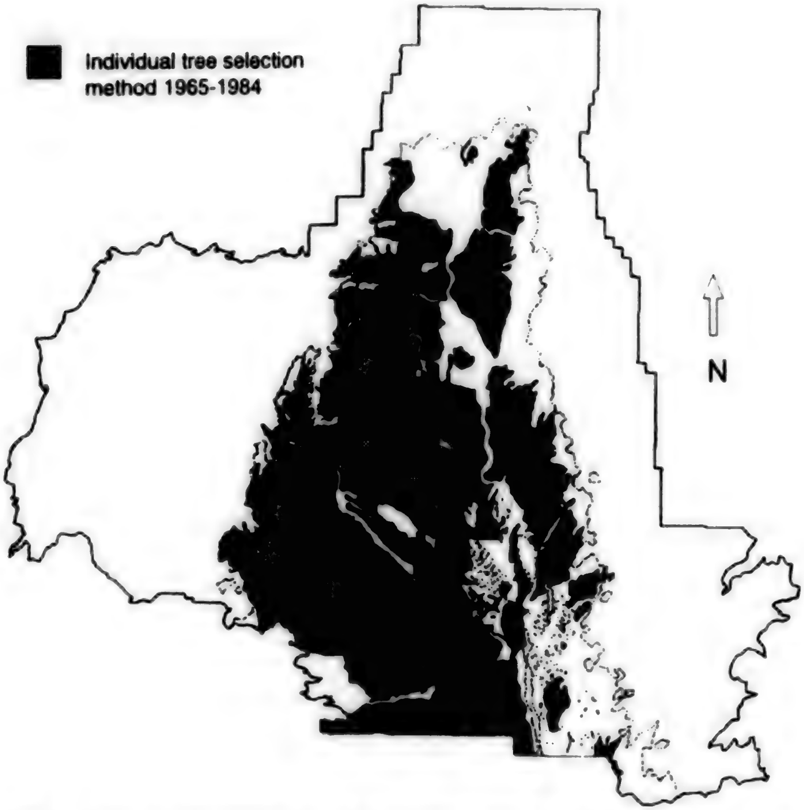

Fig. 5. Areas of the North Kaibab Ranger District (NKRD) harvested using the individual tree selection method: 1965–1984.

Figure 7 relates Forest Service designated critical habitat for the Mexican spotted owl and Forest Service northern goshawk territories (U.S. Forest Service 1994, U.S. Department of the Interior 1995).

The northern goshawk's existence on the plateau has long been noted. Rasmussen's (1941), flora and fauna assessments of the late 1930s, characterized the northern goshawk population to be sparse and have spotty distribution in the yellow pine and spruce-fir forested areas of the plateau. He noted that:

> "The Goshawk is a bird of considerable importance in the interactions of this community. Only its scarcity prevents it from being a major influence. Although Arizona is considered to be the extreme southern tip of their breeding range, birds were seen during

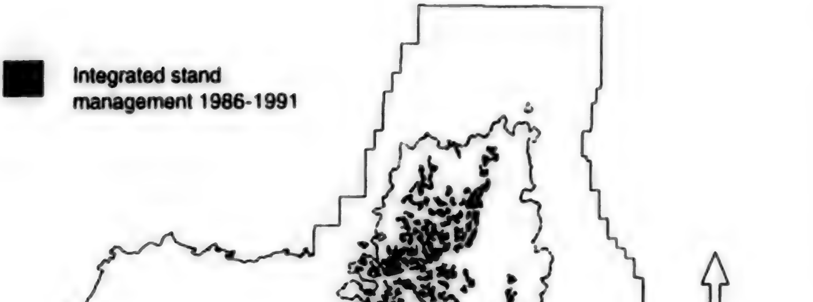

Fig. 6. Areas of the North Kaibab Ranger District (NKRD) harvested under integrated stand management: 1986–1991.

all months over three summers of study. It was estimated in 1931 that there was one Goshawk per five sections." "Observation of food habits showed that adult hawks feed mostly on birds, but caught rabbits, the mantled ground squirrel, the Fremont chickadary and the Kaibab squirrel" (Rasmussen 1941).

Today, the Forest Service is managing for two northern goshawks per four sections (2,880 acres), or one bird per 1,440 acres. This is approximately twice the number of birds by area estimated by Rasmussen (1941) (one per 3,600 acres). Surveys to date have located eighty nesting pairs on 240,000 acres, or one bird per 1,500 acres. Although there is no effective method to compare the accuracy of bird counts in the two assessments, one

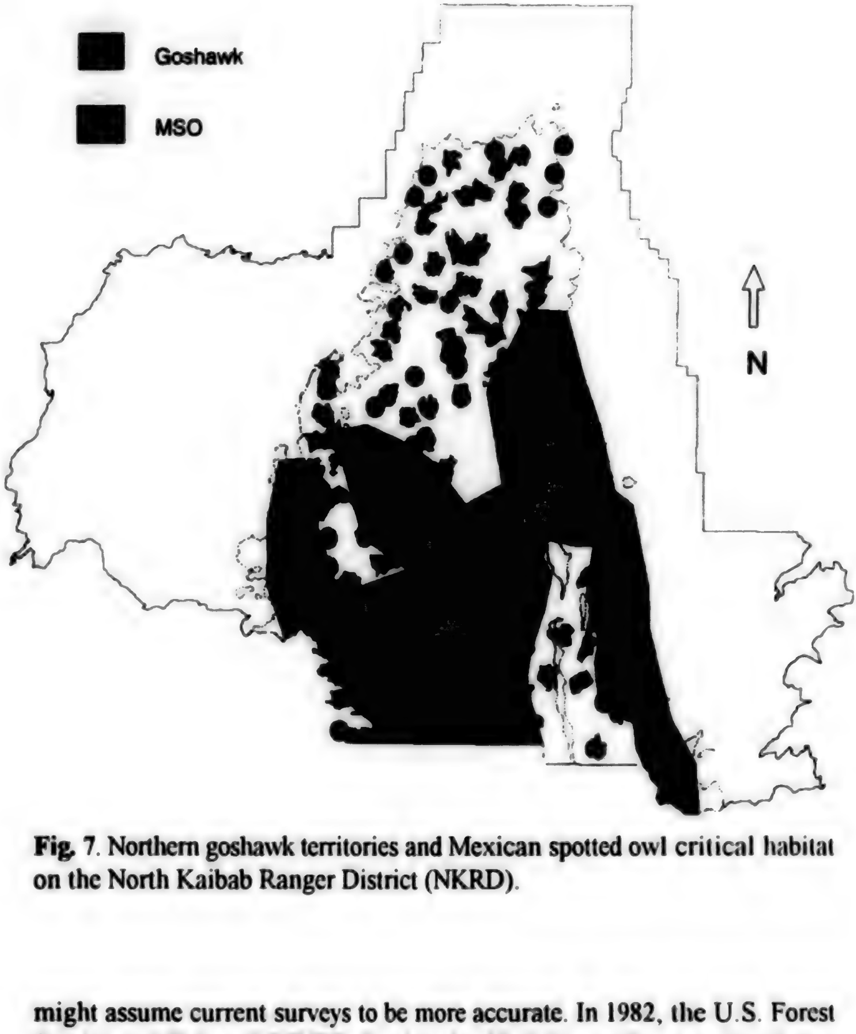

Fig. 7. Northern goshawk territories and Mexican spotted owl critical habitat on the North Kaibab Ranger District (NKRD).

might assume current surveys to be more accurate. In 1982, the U.S. Forest Service and Fish and Wildlife Service classified the northern goshawk as a sensitive species, requiring further study (U.S. Forest Service 1994). Increased research since that time includes work by Reynolds (1989), Crocker-Bedford and Chaney (1988), and Kennedy (1989), who have developed energy, nesting and feeding information on the species. Research by Crocker-Bedford and Chaney (1988), was extrapolated temporally and spatially to conclude that the northern goshawk population was declining, and that overstory removals were a probable factor in species decline. Reynolds (1989) concluded that northern goshawks were at their social density peak on the North Kaibab. A comparison of the Rasmussen (1941) assessment and current surveys would indicate increases in bird density.

The northern goshawk is the largest member of the Accipiter family, and occupies coniferous and deciduous forest types. Its long tail and short round wings are adaptive to hunting forest areas. The diet is varied but includes 4.2 to 5.3 small to medium birds and mammals per day (U.S. Forest Service 1992). The northern goshawk is widely dispersed over all major forest types which contain a wide range of forest ages and successional stages due to fire, disease, insects, and logging. How the northern goshawk uses these different forest conditions is not fully known (Reynolds 1989, U.S. Forest Service 1992). Knowledge of limited use of young dense stands does exist, due primarily to bird size (Fisher 1986). Also, although the northern goshawk takes over 50 different species, more knowledge is needed about the structure and composition of habitats used by foraging northern goshawks (Reynolds 1989, Kennedy 1991).

With more information desired, continuing ongoing surveys of the population have been implemented on the plateau during the 1990s. Areas noted in Fig. 7 show distribution of nesting sites on the plateau and include the 600 acre protected zone around the nests and 5,400 acre post-fledging area called for in management guidelines (U.S. Forest Service 1992). Within 180 acres of the 600 acre zone, little management action can occur in the overstory or understory. In the remaining 420 acres some management is allowed. The additional 5,400 acres is for post-fledging use by offspring. During the nesting period little overstory management activity is permitted in the general nest locations.

A second species, the Mexican spotted owl, has been under study in the Southwest for a shorter period of time than the northern goshawk. There have been extensive studies of the northern spotted owl in the Pacific Northwest, but questions exist regarding the transferability of research from the study of northern spotted owls to Mexican spotted owl habitat. Although some concern existed over the need for better definition of the Mexican spotted owl's critical habitat in the Southwest, its listing in 1994 precipitated the requirement for critical habitat establishment. That critical habitat is pervasive, especially in the recommended requirements for species nesting, fledging and foraging requirements (U.S. Department of the Interior 1995). Figure 7 shows the area on the Kaibab Plateau which was proposed in 1995 as critical habitat for the Mexican spotted owl (U.S. Department of the Interior 1995). Vegetative types represented include pinyon-juniper, canyons dominated by mixed species hardwood and softwood, ponderosa pine, and mixed conifer and spruce-fir type forest ecosystems. Most of the area is ponderosa pine and mixed conifer cover types.

Research continues on the Mexican spotted owl in the Southwest and the Kaibab Plateau. Also continuing are inventories which locate adult individuals or pairs and/or nest sites. Between 1990–1994 numerous intensive inventories of the entire Kaibab Plateau were conducted to locate nest sites and/or adults within the habitat. These intensive surveys have failed to locate Mexican spotted owl nest sites (J. R. Ellenwood 1996, Kaibab National Forest, Williams, Arizona, personal communication).

A review of scientific literature to date do not document sightings of the Mexican spotted owl on the plateau. Rasmussen (1941) in his intensive study failed to identify the species on the plateau over a 3–year period.

Implications of Current Management Direction

We have evaluated changes in the North Kaibab overstory through the period 1900–1994, illustrating increasing densities in trees smaller and larger than 6" dbh. There have been significant removal of overstory by harvests, thinnings, and natural mortality. Documented harvest activity from the early 1900s to 1993 have accounted for over 1.4 billion board feet of harvests. In addition, many trees have been lost to natural mortality. However, recruitment of new trees through regeneration has greatly exceeded removals and natural losses from the overstory, so much so, that average number of trees per acre above 6" dbh has risen from 45.3 in 1910 to 115 in 1993, and trees below 6" dbh have increased from 107 to over 900 per acre.

The question of what level of tree density is desirable is a social issue. Any public land desired future condition will create an array of social benefits and costs or tradeoffs. Forest managers and the general public must evaluate these tradeoffs to determine the preferred management direction.

Forest health specialists, fire ecologists, and conservation biologists have determined that increasing densities in western ponderosa pine forest ecosystems are degrading these ecosystems and placing increased acreages at greater risk to insects and diseases and destructive wildfires (Sampson and Adams 1994). In general, increased densities reduce forest health and diversity and create ecosystem conditions that are not sustainable.

Several authors cite the following conditions to result from increased densities (Brown et al. 1974, Schubert 1974, Rogers et al. 1984, White 1985, Covington and Moore 1994).

- reduced tree growth
- stagnated nutrient cycles
- increased insect and disease
- decreased forage
- increased fuel loads
- decreased native flora
- increased crown wildfire
- decreased on-site water

These specialists and others have noted increased tree densities to cause greater risk to the entire forest ecosystem. Stand density index is one measure used to evaluate overstory densities and the potential threats they impose on the forest ecosystem (Schmid et al. 1994). Schmid et al. (1994) proposed using three growing stock levels as guides for managing mountain pine beetle in the Black Hills of South Dakota.

Generally, three levels of density are proposed by Schmid et al. (1994), as interpretive guidelines for ecosystem risk: 0–34, 34–54, and 54% of SDI. SDIs below 34 are not considered threatening. That is, densities at and below this level do not seem to create unhealthy tree competition and measurable degradation to the ecosystem. Moderate SDIs from 34–54 result in increased measurable stress that begins to manifest itself in decreased health and diversity and threats to sustainability. High SDIs above 54 place the forest ecosystem at risk in many categories. Increased competition for light and nutrients, increased moisture stress in plants, increased outbreaks of insect and disease, and greater risk of destructive wildfires are examples of threats to sustainability.

There are a number of acreages on the NKRD that fall into moderate and high risk densities, as regards Schmid et al. (1994) stand density index risk ratings (Fig. 8). Over 60% of the ponderosa pine forest is moderate to high risk and 33% is high risk. That tree densities have increased radically on the NKRD in the past 100 years means little to most people. However, these increases in tree densities could pose major ecosystem management problems on the Kaibab Plateau. The forests of the Kaibab Plateau appear to be on a path similar to that of the Blue Mountains of Oregon (Sampson and Adams 1994). Forest ecosystems in the Blue Mountains have become so degraded due to high tree densities, that a national program has been implemented to save extensive forest watersheds from destruction by wildfire catastrophes (Sampson and Adams 1994).

In this paper we have described increases in overstory tree densities on the North Kaibab that appear unwarranted, especially in view of existing scientific knowledge. It would seem prudent for managers to initiate management actions to mitigate the ecosystem impacts of increased densities.

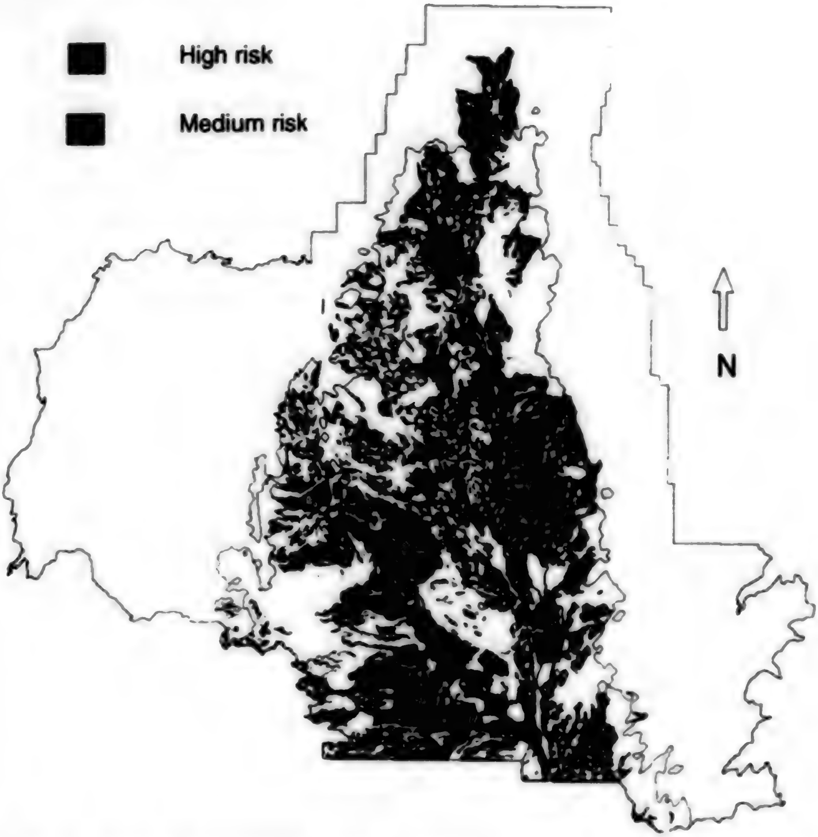

Fig. 8. Areas of the North Kaibab Ranger District (NKRD) classified as medium to high risk using stand density index as a relative measure of stand density.

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Changes from 1876 to 1994 in a Forest Ecosystem Near Walnut Canyon, Northern Arizona

Jody P. Menzel
W. Wallace Covington

School of Forestry
Northern Arizona University
NAU Box 15018
Flagstaff, Arizona 86011

Abstract. A central concept in adaptive ecosystem management is the use of the range of natural variability as a reference for developing and assessing management objectives and strategies. Using the range of variability as a reference requires that the conditions which prevailed prior to Euro-American settlement, which commenced in the mid- to late-19th century in the West, be described and quantified. We used dendroecological techniques to estimate changes in forest structure since Euro-American disruption of the natural disturbance regime in a *Pinus ponderosa-Quercus gambelii* woodland on the northern rim of Walnut Canyon in northern Arizona. The reconstruction of the 1876 stand structure showed an increase in density of trees greater than 10 cm diameter at breast height (dbh), or greater than 10 cm diameter at root collar (drc) for nontimber species, from 72 stems/ha in 1876 to 333 stems/ha in 1994. Total basal area for trees larger than 10 cm increased from 9.0 m^2/ha in 1876 to 19.1 m^2/ha in 1994, primarily due to a greater number of trees in smaller size classes. Overstory composition also changed since 1876. At that time *Pinus ponderosa* stems represented an estimated 80% of the basal area of all trees larger than 10 cm, a proportion which decreased to 68% in 1994. *Quercus gambelii* increased from less than 5% of total basal area in 1876 to over 15% in 1994, *Pinus edulis* increased from 2.5% to nearly 5%, and *Juniperus* spp. increased from 12.7% to 15%.

Changes in forest structure associated with Euro-American settlement previously have been documented in pure and mixed western pine ecosystems. Results from the Walnut Canyon area demonstrate that similar changes also occurred on marginally productive limestone soils near and within the ecotone between ponderosa pine forests and pinyon-juniper woodlands.

Key words: Ecosystem management, Euro-American settlement, fire suppression, pine-oak woodland, presettlement, range of natural variability.

Research Objectives

Although humans have had considerable impacts on the interior forests and woodlands of western North America for millennia (Kay 1995). ecosystem changes since the mid-19th century Euro-American settlement of the interior western U.S. are unprecedented within such a relatively brief period of time. Livestock grazing, fire suppression, timber and other resource extraction, and landscape modification are perhaps the most significant of the Euro-American activities which caused these changes in interior western ecosystems. Changes since Euro-American settlement include a greater number of trees in smaller size classes, shifts in species composition, and tree invasions into historically unforested areas. A few of the actual and potential adverse effects associated with these changes are increases in the risk and intensity of wildfires, increases in the incidence and severity of forest pathogen outbreaks, decreases in stream flow, and shifts in habitat quality (Covington et al. 1994). Resource managers are increasingly concerned with mitigating or reversing the adverse environmental impacts of Euro-American settlement as these problems become manifest (U.S. Forest Service 1993, Kaufmann et al. 1994).

Ideally, resource managers would mitigate adverse effects associated with anthropogenic impacts by instituting management practices based on a comprehensive understanding of the systems and interactions involved. In reality, the complexity of ecosystems precludes such an approach. In the absence of a comprehensive understanding of ecosystem functions, a proposed approach is to use the environmental conditions which prevailed in an area prior to significant anthropogenic impact as a reference with which to design and assess management goals and strategies (Bonnicksen and Stone 1985, Monnig and Byler 1992, Kaufmann et al. 1994). An approach based on this range of natural variability, or RNV (Swanson et al. 1994), is propitious because: (1) native species, including those listed under Endangered Species Act of 1973, have evolved in concert with the RNV, and (2) many forest health problems, such as unnatural insect and disease outbreaks and the risk of increasingly destructive fire, are due to post-settlement departures from the RNV (Covington et al. 1994, Harvey 1994).

Before management practices or goals which use the RNV as reference conditions can be instituted, managers must know what constituted the RNV over the spectrum of ecosystems (Covington and Moore 1994a, Morgan et al. 1994). The research described here directly addresses this problem. The purposes of this research are to: (1) estimate the pre-Euro-American settlement forest structure of a ponderosa pine (*Pinus ponderosa*)-Gambel oak (*Quercus gambelii*) woodland near Flagstaff, Arizona, in terms of tree composition and size distributions; (2) quantify the changes which have occurred in the area since Euro-American settlement; and (3) compare changes with regard to different management histories in the area. Our discussion of the research results will explore management implications suggested by the study.

Ponderosa Pine Forest Ecology

In northern Arizona, ponderosa forests have been well established for at least the past 4,000 years (Cole 1990). Regional climate changes, including more frequent lightning strikes and ignitions coincident with the advent of the Arizona monsoon weather pattern, likely contributed to the ascendancy of fire-resistant ponderosa pine on the montane Colorado Plateau (Anderson 1989). Packrat midden macrofossils from within Walnut Canyon suggest that the vegetative composition of our study area has changed little in the past 5,000 years (Murdock 1994).

Native Americans undoubtedly influenced the character of forest and woodland ecosystems, but the magnitude of their impact is subject to debate (Kay 1995). Aboriginal broadcast burns, cultivation, and construction had at least localized ecosystem effects. For example, the appearance of yucca (*Yucca* spp.) macrofossils in packrat middens only after Sinagua colonization of Walnut Canyon may reflect an aboriginal modification of the local vegetation (Murdock 1994). The direct impacts of aboriginal settlement in the Walnut Canyon area ceased with the abandonment of the Walnut Canyon cliffhouses about 700 years ago (Short 1988), but some Native American impacts, such as fire ignitions, may have continued sporadically (see, e.g., Cline 1976). For our purposes, we accept a definition of the RNV which incorporates the influence of Native Americans prior to Euro-American settlement (cf., Parsons et al. 1986, Bonnicksen 1994).

Empirical and historical evidence suggests that the presettlement ponderosa forest landscape was dominated by groups of old-growth pines with few seedlings, saplings, and poles. Cooper (1960) summarizes numerous early descriptions of the Arizona pine forest as follows: "The forest was decidedly open and park like. Reproduction was present but not abundant, and in many areas was markedly deficient. Grass was abundant, but not universal." Recent quantitative reconstructions of presettlement ponderosa pine forest structure corroborate early qualitative descriptions (Covington and Moore 1994a,b).

Relatively frequent surface fires maintained the open forests dominated by older trees which characterized the presettlement landscape. Early disruption of this disturbance pattern was primarily due to livestock grazing and the corresponding reduction in fine fuels rather than to active fire suppression (Harrington and Sackett 1992). Several fire disturbance history studies in the Southwest show a marked decrease in fire frequency around the turn of the century, coincident with increasing Euro-American livestock introductions (Swetnam 1990). Studies in northern Arizona reflect the relatively frequent fires in the area prior to Euro-American settlement. In the years 1785–1876 the average fire return interval was 2.5 years, with a maximum interval of 8 years, at Chimney Springs north of Flagstaff (Dieterich 1980a). In 1750–1898 the average fire return interval was 2.9 years, with a maximum interval of 10 years, at Limestone Flats south of

Flagstaff (Dieterich 1980b). Dated fire-scar samples from the Walnut Canyon area suggest that its ponderosa pine forests experienced fire return intervals similar to others in the region prior to 1900 (Swetnam et al. 1990).

Study Area

Physical Description

The study area consists of six contiguous sections of approximately 259 ha (640 acres) each on the north rim of Walnut Canyon in northern Arizona (Fig. 1). These sections are numbered 21, 22, 23, 26, 27, and 28, Gila and Salt River Baseline and Meridian. Within this study area, the U.S. Forest Service manages public lands within sections 21, 23, and parts of 26 and 27. The State of Arizona Land Department manages sections 22 and 28, and the U.S. Park Service manages the southern portion of section 26.

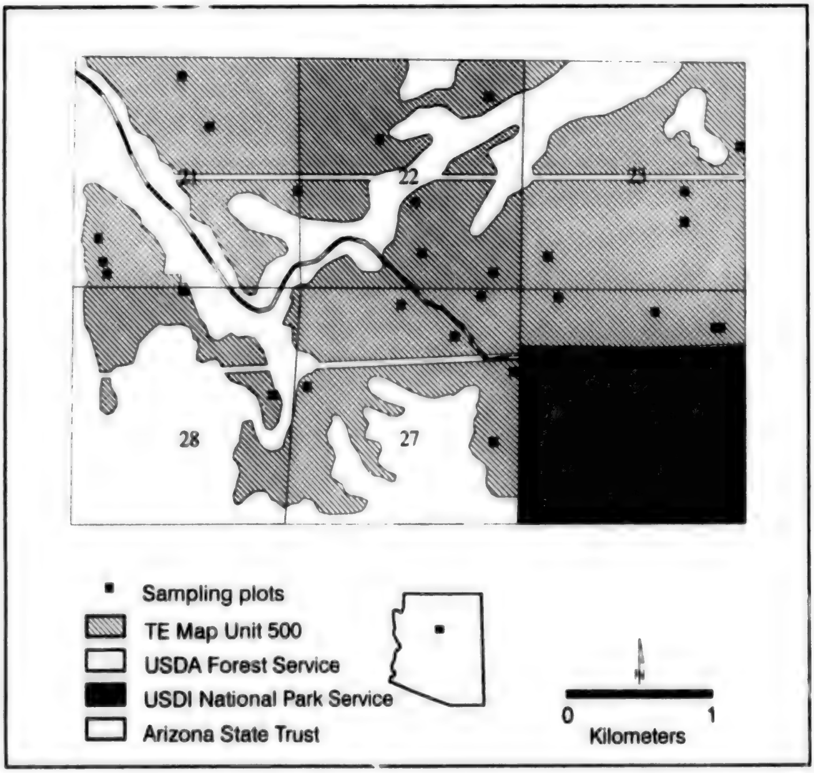

Fig. 1. Map of study area near Walnut Canyon National Monument, northern Arizona. The numbers 21–23 and 26–28 correspond to section numbers. Diagonal hatching represents land within the U.S. Forest Service's TE map unit 500 classification.

Sample plots were located within an elevational range of about 2,000 m to 2,150 m above sea level. Soils are shallow, well-drained derivatives of the Kaibab Limestone formation, with some sandstone components. Average annual precipitation at Walnut Canyon National Monument is 45 cm, with about 16 cm in the form of winter snowfall; average daily temperatures range from 11° C to 30° C in the summer and -8° C to 7° C in the winter. Summer precipitation falls mostly during July, August, and September, when thunderstorms develop almost daily. Winter precipitation is extremely variable, with most snow falling between late November and early March (U.S. Soil Conservation Service 1975). Average annual snowfall is 140 cm (U.S. Park Service 1992). The growing season in Walnut Canyon National Monument is 150 days (Short 1988).

Study plots were located within the *Pinus ponderosa-Poa fendleriana-Quercus gambelii* biotic community, and within the ecotone representing the gradation of this community into the *Pinus edulis-Juniperus monosperma-Bouteloua gracilis* biotic community (Brown 1982) as elevations drop to the north and east within the study area. Gambel oak is common throughout the area, but is replaced by pinyon pine and junipers in the ecotone marking the transition from ponderosa pine forest to pinyon-juniper woodlands. Juniper species found in the area, in order of their present-day occurrence in the sample plots, are Utah juniper (*J. osteosperma*), alligator juniper (*J. deppeana*), one-seed juniper (*J. monosperma*), and Rocky Mountain juniper (*J. scopulorum*).

Local Land Use History

Local changes in forest structure reflect changes in the patterns and relative impacts of human land use, so a history of those uses is instructive. The San Francisco Peaks area of northern Arizona has been visited or occupied by Native Americans sporadically since at least 4000 B.C. From about A.D. 1125 to A.D. 1250 a community of Native Americans of the Sinagua culture group lived in cliff dwellings within Walnut Canyon. The cliff dwelling community was relatively small, occupying at most 300 rooms within the 87 sites in the canyon, and they left the area entirely by about 1,300 (Short 1988). Native Americans continued to travel in the area following the Sinagua abandonment, and explorers and missionaries of European descent occasionally forayed through northern Arizona in the three centuries following Coronado's expedition in 1540 (Cline 1976). Human impact was minimal until the 1850s, however, when about 551,000 sheep were driven from New Mexico to California. One of the two major driveways during this decade passed through the Flagstaff area along the route of the Beale wagon road, which passed within 3 km of the Walnut Canyon study area (Haskett 1936). In the decades after Beale's last expedition in 1859, the wagon road was used by hundreds of Euro-Americans.

The first Euro-American to permanently settle in the Flagstaff area was a sheep rancher, Thomas Forsythe McMillan, who arrived no later than May 1876. This also was the year in which the flag was raised which gave the community its name (Cline 1976). It was the last year marked by frequent fires in the Walnut Canyon area (Swetnam et al. 1990), and it coincides with Dieterich's (1980a) evidence for the last fire at Chimney Spring. Thus, 1876 is an appropriate year with which to define the advent of Euro-American settlement in the area.

Livestock husbandry, primarily sheep ranching, was the primary Euro-American activity in the Flagstaff area until the establishment of the Ayer Lumber Company in 1882 (Cline 1976). By 1891 there were about 110,000 head of cattle and 9,000 horses competing with 270,000 sheep in the Flagstaff area (Cline 1994). In 1904, Leiburg et al. described the range around Flagstaff as "eaten or sheeped out," and reported that the grazing value of the township containing the study area was "yet moderate, but [it] will not last many years longer. Some of the northern sections... now chiefly produce coarse weeds."

Sheep were replaced by cattle in the Walnut Canyon area in the mid–1950s. In 1991, 1,160 cattle were permitted within two extensive allotments which extend into portions of the study area outside Walnut Canyon National Monument. Range conditions in the study area in 1991 were rated fair to good, with a static or upward trend (U.S. Forest Service 1991).

All the land within the study area, with the exception of lands patented under the Preemption or Homestead Acts, was public domain administered by the Department of the Interior until the Atlantic and Pacific Railroad was granted the odd-numbered sections in the 1880s. As public domain, the land generally was closed to timber harvest. Timber trespass by early settlers and loggers probably was frequent to the point of being commonplace, however (Matheny 1975). Many of the oldest stumps in the study area, some of which are axe-hewn, probably date to unregulated cutting by early settlers and loggers prior to the large-scale commercial harvests which commenced with the establishment of the Ayer Lumber Company in 1882.

The Arizona Lumber Company, successor to the Ayer Lumber Company, purchased by 1889 all timber on all 868 odd-numbered sections owned by the Atlantic and Pacific Railroad, including timber within sections 21, 23, and 27 of the study area. In 1890 the even-numbered sections in the area, with the exception of section 26, were granted to the State of Arizona under the Lieu Lands Provision of the Territorial Enabling Act of 1863.

The odd-numbered railroad grant sections had been heavily harvested by 1902. Less than 2,000 board feet per acre remained in sections 21 and 27, and section 23 had been clearcut. In contrast, between 2,000 and 5,000 board feet per acre remained within the unharvested sections 22, 26, and 28 (Leiburg et al. 1904).

In 1902, the Atchison, Topeka and Santa Fe Railroad (formerly the Atlantic and Pacific Railroad) began to exchange its odd-numbered sections within the San Francisco Peaks Forest Reserve for land outside the Reserve under the lieu lands provision of the 1897 Organic Act. Sections 21, 23, and 27 were revested in 1904 and came under the management of the U.S. Department of Agriculture's Bureau of Forestry, which became the U.S. Forest Service in 1905.

Walnut Canyon was established as a National Monument in 1915 under the management of the U.S. Forest Service. It came under U.S. Park Service management in 1934. Scattered ponderosa pine stumps within its boundaries attest to unregulated cutting and timber trespass prior to the protection afforded by Monument status, and stumps of other species reflect illegal fuelwood gathering, which was curtailed with the completion of an effective boundary fence in 1977. The fence also eliminated the common problem of trespass grazing within the Monument.

The state-managed sections 22 and 28 were harvested in 1914–1916 by what had become known as the Arizona Lumber and Timber Company. After then, timber and fuelwood harvests in the area were relatively light. Selected declining trees were harvested on both state and U.S. Forest Service-managed lands in the area in the early 1970s, and an oak fuelwood sale was conducted in state-managed Section 22 in 1988. Other management activities within the study area include some small (less than 4 ha) prescribed burns within Walnut Canyon National Monument in the 1980s, followed by a more aggressive prescribed burning program of 8 ha and greater annually within the Monument beginning in 1995. During this century, suppression has extremely confined the occurrence, areal extent, and environmental effects of wildfires in the area (Swetnam et al. 1990). Due in part to its proximity to Flagstaff, the area is much used by hikers, bicyclists, equestrians, and recreational motorized vehicle enthusiasts, as well as by illegal trash dumpers and firewood gatherers. Local advocates for protection of the area, organized as the Friends of Walnut Canyon, influenced a 1991 decision to withdraw sawtimber harvests scheduled for 1996 on the U.S. Forest Service-managed sections in favor of a management alternative which emphasized scenic, recreation, and wildlife values.

On 12 November 1996 President William Jefferson Clinton signed into law the Omnibus Parks and Public Lands Management Act, which expanded Walnut Canyon National Monument by 539 ha. About 65 ha of this transferred land, the SE 1/4 of section 27, is within the study area. This expansion will challenge the Monument's land managers to devise management strategies reflecting the NPSs preservation mandate in an area formerly governed by the U.S. Forest Service's multiple-use mandate.

Methods

We used classifications from the U.S. Forest Service Terrestrial Ecosystem Survey (TES) (U.S. Forest Service 1986) to exclude gross site differences between sample points while sampling within a large proportion of the greater study area (cf. Covington and Moore 1994a,b). This classification system represents a coarse-filter approach (*sensu* Kaufmann et al. 1994); it describes ecosystem attributes at a level of detail which incorporates considerable variation while still retaining definitive similarities. The TES classifies ecosystems with similar soil, vegetation, and slope properties into similar Terrestrial Ecosystem (TE) map units. TE map unit 500 is characterized by Mollic or Lithic Eutroboralfs, or Udic Ustochrepts soils; limestone bedrock; a High Sun Cold climate classification; overstory vegetation dominated by ponderosa pine, with pinyon pine, juniper, and Gambel oak secondary; and slopes ranging from 0 to 15%. We randomly located 30 sampling locations within TE map unit 500, the most extensive unit within the study area, by assigning numbers to all potential sampling locations and choosing for sampling those locations whose numbers appeared first on the random number generator of an HP-71 scientific calculator.

In order to quantify differences in forest structure between management units, we ensured that the number of sampling locations in each management unit was proportional to the area of TE map unit 500 within each management unit. Thus, 20 plots were located on U.S. Forest Service-managed land, seven were located on Arizona state land and three within Walnut Canyon National Monument.

At each sampling location, we established a 40 m x 40 m plot to measure presettlement forest structure and a 20 m x 20 m nested subplot to measure present forest conditions. The northeast 20 m x 20 m quadrat within each 40 m x 40 m plot represented the current-conditions subplot. Within the current-conditions subplots, we recorded the species and location of all live trees, snags, stumps, and fallen trees. For ponderosa pine, diameter was measured at breast height (dbh = 1.37 m). Diameter was measured at root collar for species other than ponderosa pine (see Born 1985). Increment cores were taken at 20 cm above ground level from all live trees with a dbh or drc of 10 cm or greater.

We classified standing trees into one of seven snag condition stages according to characteristics described in Maser et al. (1979). Snag decomposition stages and their associated characteristics are: Stage 1 (healthy live trees), Stage 2 (declining live trees), Stage 3 (recently dead trees), Stage 4 (loose bark), Stage 5 (clean), Stage 6 (broken), and Stage 7 (decomposed). We also used five condition classes described by Maser et al. (1979) to classify fallen dead material, based on log characteristics such as the amount of bark present, the presence or absence of small (< 3 cm) twigs, the texture of the wood, the cross-sectional shape (round or oval) of the log, the color of the wood, and the portion of the log resting on the ground. Stumps were classified according to the snag criteria.

Sampling procedures on the remaining three-fourths of the 40 m x 40 m plots were identical to those used on the 20 m x 20 m present conditions subplots, with the exception that only those trees, living and dead, which appeared to have established during or before 1876 were measured. A living tree was judged presettlement according to criteria modified from White (1985), i.e., all ponderosa pine trees greater than 37 cm dbh, and all ponderosa pine trees smaller than 37 cm but exhibiting yellow bark, were measured. Living trees of other species were measured if diameter at root collar was equal to or greater than 25 cm; this criterion was based on field examinations of increment cores, which indicated that trees which had established during or before 1876 would rarely fail to reach 25 cm drc in 1994. We adjusted the diameter criteria for establishing whether a tree was presettlement or not upward or downward if field examination of several increment cores suggested it was prudent to do so. The minimum size criteria for determining whether or not to measure dead material within the presettlement subplots were the same as the diameter criteria for live trees (37 cm for ponderosa pine, 25 cm for other species). However, since it was usually impossible to determine presettlement origin in the field, we subjectively but conservatively measured any and all material which we considered could have been of presettlement origin based on its degree of decomposition and diameter.

We mounted and surfaced the increment cores and counted annual rings on all samples under a microscope to estimate tree age and measure the 1876–1994 radial increment, if present. All ponderosa pine tree samples were cross-dated (Stokes and Smiley 1968) by comparing them to a tree-ring width chronology from the International Tree-Ring Data Bank at the National Geophysical Data Center in Boulder, Colorado, developed by Graybill and Rose (1989) for the Walnut Canyon area.

We determined current (1994) forest structure and species composition directly from the diameter measurements and counts of live trees within the 20 m x 20 m subplots, extrapolated to a per-ha basis. We used less straightforward dendrological techniques and mathematical models to determine the 1876 forest structure and composition.

For ponderosa pines, if an 1876 growth increment existed and the tree pith was present or its location could be estimated from the increment core, we measured the diameter from the pith to this 1876 increment. We then used a regression equation developed by Hann (1976) to correct this measurement from 1876 diameter inside bark at stump height (dsh) to 1876 diameter outside bark at breast height.

Determining the 1876 dbh of ponderosa pines with incomplete cores was more complicated. These were ponderosa pine cores for which the location of an absent center pith could not be estimated from the increment core. To estimate 1876 dbh of possible presettlement ponderosa pines smaller than 37 cm dbh with incomplete cores, we used the ponderosa pine diameter mean annual increment (DMAI) as calculated from all sampled trees with complete cores, and subtracted this value 118 times from 1994 dbh. For ponderosa pine trees 37 cm dbh and larger with incomplete cores, we used measurements from complete cores to develop a regression equation which estimated the expected value of 1876 dbh based on 1994 dbh.

When we had complete cores from oak and juniper trees of obvious presettlement origin, we determined whether an 1876 growth increment was present by counting rings. We were unable to develop a predictive 1876-1994 BAI model for these species because of the small number of complete presettlement core samples, the uncertainty of the presettlement radial diameter measurements for complete cores, and the lack of species-specific formulae to correct from diameter at root collar outside bark to diameter at stump height inside bark. Instead we used annual growth estimates from Rogers et al. (1984) to estimate 1876 drc or, for those species for which Rogers et al. (1984) did not provide annual growth estimates, we used the DMAI as calculated from our data set.

To determine the 1876 dbh of dead material, we first estimated the year in which the tree had died, then subtracted modeled growth between 1876 and the year of death. We used both published decomposition rates and harvest dates to estimate year of death for dead material. Rogers et al. (1984) provided locally calibrated estimates of the rates at which standing dead trees move from one snag condition stage to another, based on data from the Fort Valley area about 20 km northwest of the Walnut Canyon study area. Cunningham et al. (1980) provided descriptions of snags and their ages from the same general area as that of the Rogers et al. (1984) data; we used the Cunningham et al. (1980) descriptions to estimate ages of recently dead trees.

Year of death for stumps was inferred from harvest records. Where records were unavailable, death year was estimated using the snag decomposition rates. Ponderosa pine stumps in snag condition stages 3 and 4 were assigned a 1970 harvest date. Ponderosa pine stumps in snag condition stages 6 and 7 in what are now state land sections were assigned a harvest year of 1915, while those in what are now U.S. Forest Service-managed sections were assigned a harvest date of 1901. Gambel oak stumps within state land sections and in snag decomposition stages 3 or 4 were assigned a 1988 harvest date. Finally, we included a stump decomposition stage in the field which did not correspond to any of the snag condition stages in Maser et al. (1979), representing stumps in a state of decomposition more advanced than those which we otherwise would have classified as stage 7 stumps. These "stage 8" stumps were sometimes marginally identifiable as stumps at all, and sometimes showed evidence of being ax-hewn. We conservatively assigned these ancient stumps a harvest year of 1890, prior to the known commercial harvest dates but within the period of accelerating European-American settlement which followed the arrival of the railroad in 1882.

We estimated years of death for fallen trees by applying decomposition rates in Rogers et al. (1984) and to logs in decomposition classes described in Maser et al. (1979).

Results

Comparison of 1876 and 1994 Forests

Our research shows the following changes in forest structure and composition for trees larger than 10 cm diameter since 1876, our base comparison year: (1) increases in density (stems/ha) for all species in the area, (2) a shift in structure toward trees in smaller diameter classes, and (3) a shift in composition toward nontimber species.

Tree density increased from 72 stems/ha in 1876 to 333 stems/ha in 1994 (Fig. 2). Virtually all of this increase is in diameter classes less than 40 cm. Note that Fig. 2 reflects no trees larger than 80 cm in 1994. Although none of these larger trees were observed in the current-conditions subplots, they do still occur in the area.

Changes in basal area for trees larger than 10 cm follow a similar pattern (Fig. 3). Average basal area increased from 9.0 m²/ha in 1876 to 19.1 m²/ha in 1994. Increases in basal area primarily are in the smaller size classes, with a slight increase in the 60–79.9 diameter class. Again, no trees greater than 80 cm were observed in the current-conditions subplots.

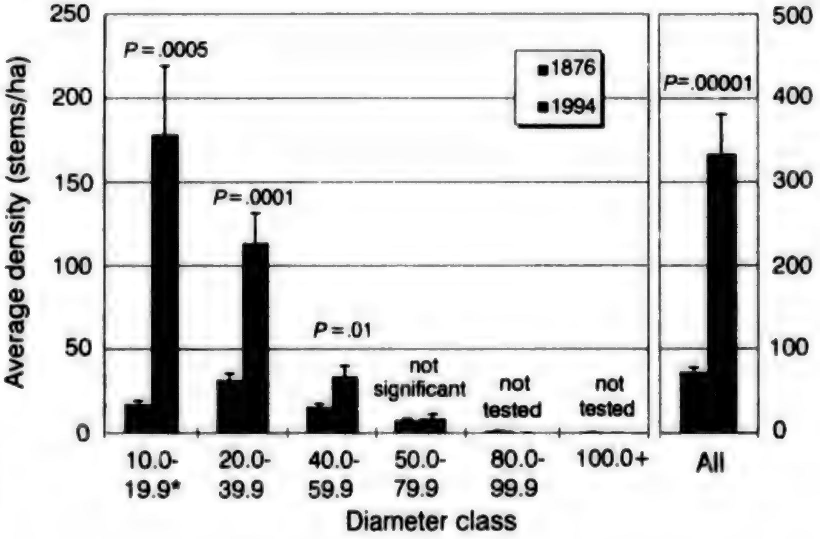

Fig. 2. Average density per 20 cm diameter class in 1876 and 1994, all species combined. Error bars are one SE of the mean. Probabilities are from two-sample separate variance *t*-tests with *n* = 30 throughout. Horizontal bars indicate statistically nonsignificant differences (*a* = .05; Bonferroni-adjusted *a* = .0125 for comparisons within diameter classes) (SYSTAT 1992). *Note unequal widths of diameter classes.

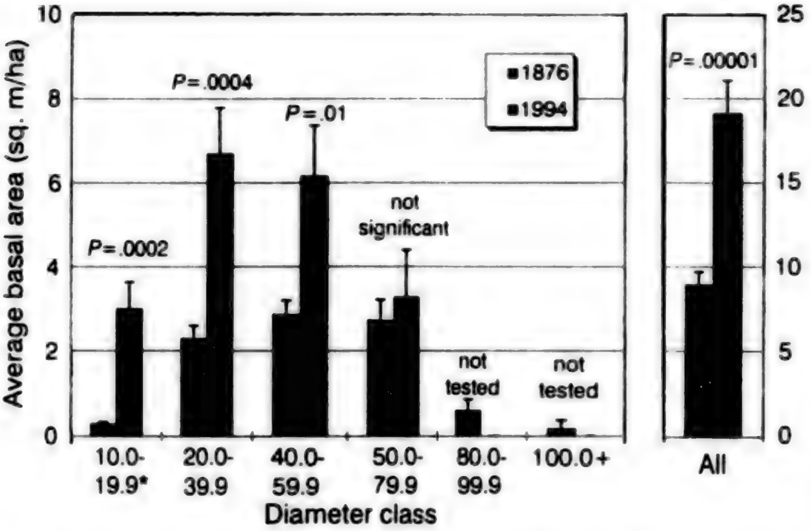

Fig. 3. Average basal area at breast height/root collar per 20 cm diameter class in 1876 and 1994, all species combined. Error bars are one SE of the mean. Probabilities are from two-sample separate-variance *t*-tests with $n = 30$ throughout. Horizontal bars indicate statistically nonsignificant differences ($a = .05$; Bonferroni-adjusted $a = .0125$ for comparisons within diameter classes) (SYSTAT 1992). *Note unequal widths of diameter classes.

Table 1 illustrates the changes in tree composition since 1876 toward greater representation by species other than ponderosa pine. In 1876, about 68% of all trees were ponderosa pine, a proportion which decreased to 55% in 1994. With the exception of Utah juniper, the proportion of the number of stems of each of the nontimber species relative to the total number of stems had increased in the years since 1876.

Changes in the proportion of total basal area occupied by each species reflect this pattern (Table 1). In 1876 ponderosa pine accounted for 80% of total basal area. In 1994 this proportion had decreased to 68%. Gambel oak increased from 4.6% of total average basal area in 1876 to 15.4% in 1994, pinyon pine from 2.5% to 4.9%, and junipers from 12.7% to 15%.

Differences in Magnitude of Changes Across Management Units

The magnitude of changes in forest structure since 1876 differed between lands managed by the three resource management agencies in the area, suggesting that different management practices over the years have had a

Table 1. Proportions of density and basal area of trees 10 cm and greater by species in 1876 and 1994.

	Average density			
	1876		1994	
Species	Average stems/ha	Percent of total	Average stems/ha	Percent of total
Ponderosa pine	54.79	67.8	250.83	54.7
Gambel oak	14.58	18.0	109.16	23.8
Pinyon pine	3.54	4.4	35.00	7.6
Utah juniper	4.79	5.9	24.16	5.3
Alligator juniper	2.91	3.6	23.30	5.1
One-seed juniper	0.21	0.2	8.33	1.8
Rocky Mountain juniper	0.00	0.0	7.50	1.6

	Average basal area			
	1876		1994	
Species	Average m^2/ha	Percent of total	Average m^2/ha	Percent of total
Ponderosa pine	7.24	80.2	12.8	67.8
Gambel oak	0.42	4.6	3.05	15.4
Pinyon pine	0.23	2.5	.98	4.9
Utah juniper	0.67	7.4	1.13	5.7
Alligator juniper	0.46	5.3	0.91	4.6
One-seed juniper	0.01	0.01	0.35	1.8
Rocky Mountain juniper	0.00	0.0	0.57	2.9

measurable effect on forest attributes. Generally, changes since 1876 on lands now managed by the Arizona State Lands Department were less pronounced than those on lands now managed by the U.S. Forest Service, while lands now managed by the U.S. Park Service experienced the greatest amount of change in density and basal area.

In 1876, average density per ha for all species combined did not differ significantly across areas now managed by the U.S. Forest Service, the Arizona State Land Department, and Walnut Canyon National Monument (Fig. 4). Increases in density since 1876 of trees larger than 10 cm in diameter were statistically significant on lands managed by the U.S. Forest Service and the U.S. Park Service, but not for Arizona State Trust lands. Agency differences were less pronounced for ponderosa pine taken alone, but the same pattern of change among the agencies is apparent. Also, although differences between ponderosa pine average densities were not statistically significant across the agencies in 1876, it is perhaps significant that Walnut Canyon National Monument, compared to the other agencies, had a smaller proportion of ponderosa pine at that time (Fig. 5). This suggests that initial species composition, combined with the differences in timber and fuelwood harvest events, could account for some of the present differences in forest attributes across the management units.

Differences in average basal area among the three management areas mirror the average density pattern, except statistical significance is lost for 1994 differences across agencies for ponderosa pine exclusive of other species (Fig. 5). The trend across the agencies is still apparent, however. Lands managed by the State of Arizona Land Department again had the least change in 1876–1994.

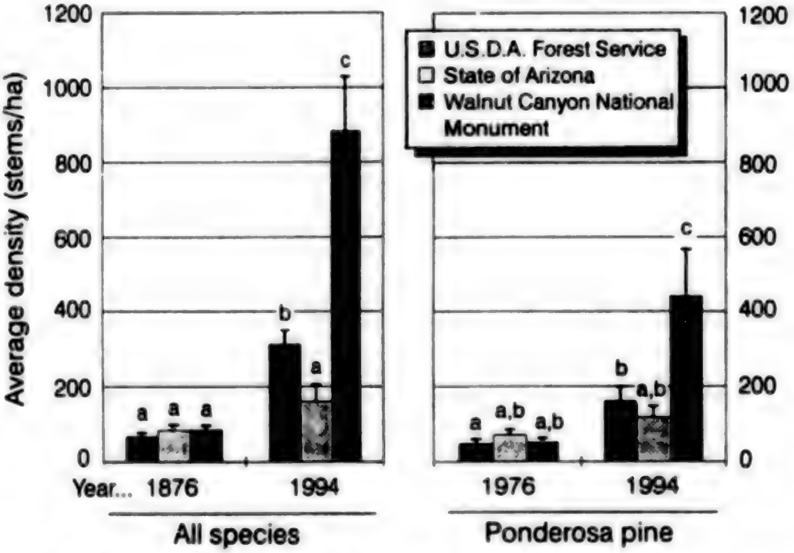

Fig. 4. Comparison of changes in average density across management agencies in 1876 and 1994. Error bars represent one SE of the mean. Same letters indicate nonsignificant differences between agencies both within and across years (*a* = .05, ANOVA weighted means model with *n* = 20 for U.S. Forest Service, *n* = 7 for Arizona State Trust, and *n* = 3 for Walnut Canyon National Monument) (SYSTAT 1992).

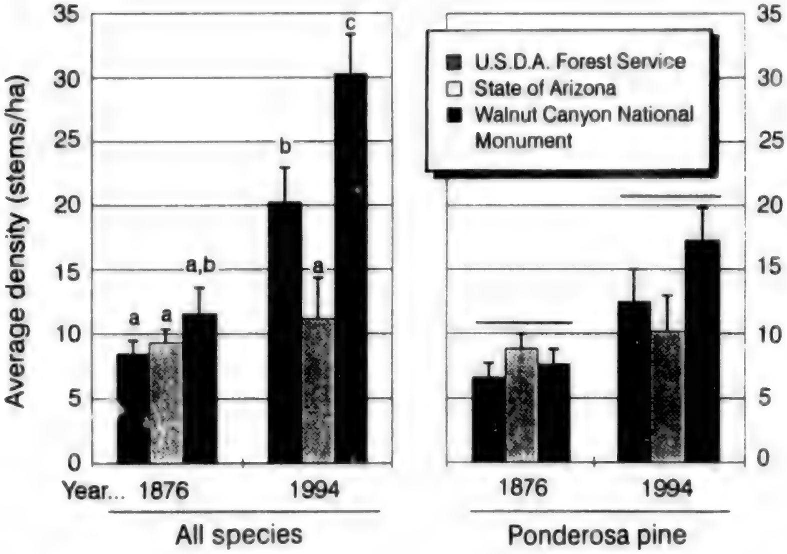

Fig. 5. Comparison of changes in average basal area across management agencies in 1876 and 1994. Error bars represent one SE of the mean. Same letters indicate nonsignificant differences between agencies both within and across years (*a* = .05, ANOVA weighted means model with *n* = 10 for U.S. Forest Service, *n* = 7 for Arizona State Trust, and *n* = 3 for Walnut Canyon National Monument). Horizontal bars indicate statistically nonsignificant differences (*a* = .05, ANOVA weighted means model) (SYSTAT 1992).

Discussion

Changes in Forest Structure and Composition since 1876

Our results suggest that the forests and woodlands on the northern rim of Walnut Canyon in 1876 were similar in appearance to ponderosa pine-type forests in other areas at that time (cf. Cooper 1960, Covington and Moore 1994a). The forests in the study area were relatively open compared to their present-day appearance, with a proportionately greater contingent of larger trees. Moreover, in 1876 most trees in all size classes were ponderosa pine. While ponderosa pine is still the dominant species in terms of basal area and sheer numbers, its dominance has diminished in the past 120 years (Table).

The magnitude of changes since Euro-American settlement are not as great in the Walnut Canyon area as those measured elsewhere in northern Arizona. Basal area increased nearly six-fold since Euro-American settlement at Bar-M Canyon and about fourfold on the North Kaibab Plateau (Covington and Moore 1994b), while total basal area roughly doubled at Walnut Canyon (Fig. 3). Ponderosa pine site quality and regeneration potential are poor in the Walnut Canyon study area (U.S. Soil Conservation Service 1975), which suggests that the magnitude of post-settlement changes in pine forest structure may be a function of site quality to some extent. Under relatively poor regeneration and growth conditions, we would expect the magnitude and the rate of increases in density and basal area which are associated with Euro-American disruption of the disturbance regime to be lower than the magnitude and rate of increases in areas with higher site quality.

The timing and extent of harvest activities also would affect the magnitude of post-settlement changes in ponderosa pine forest density and basal area. With the exception of lands within the boundaries of Walnut Canyon National Monument, the Walnut Canyon study area was logged early and heavily in the years following Euro-American settlement. Removal of much of the ponderosa pine seed source in this area of poor regeneration potential may have ensured that post-settlement increases in density and basal area associated with disturbance regime disruption would be spatially and temporally retarded relative to areas with greater regeneration potential. Differences in the magnitude of the changes in forest attributes across management unit boundaries since 1876 in the Walnut Canyon area (Figs. 4 and 5) suggest that different land-use histories and management philosophies have modulated the effects of Euro-American activities across boundaries of lands managed by the three agencies. The most pronounced of these changes are within Walnut Canyon National Monument. Although the possible influence of inherent site differences cannot entirely be ruled out, the heavier sawtimber and fuelwood harvests on Arizona state- and U.S. Forest Service-managed lands likely were most responsible for the relatively greater magnitude of change since 1876 in Walnut Canyon National Monument. The heavy harvesting of ponderosa pine overstory trees outside the Monument in the early-1900s would leave a relatively greater number of these trees within the Monument, which would result in a relatively greater seed rain. This in turn would increase the number of smaller trees within the Monument relative to other areas.

Different harvest histories can explain other differences in forest structure and composition across lands managed by the three agencies in the area. For example, sections now managed by the U.S. Forest Service have had more time to recover since the last sawtimber harvest in the early 1900s relative to Arizona state lands, which were harvested in 1914–1916. Trees which germinated in the 15 or so years between these harvest events may account for some of the differences between the U.S. Forest Service-managed lands and the Arizona state-managed lands. Also, the removal of many larger-diameter Gambel oak stems from state-managed section 22 may have moderated increases in both basal area and density since 1876 on lands managed by this agency.

Management Implications

Management practices designed to restore to some degree the presettlement attributes of the landscape in the Walnut Canyon area have much to recommend themselves. Perhaps most saliently, restoration of these attributes could inhibit or ameliorate potential adverse effects of post-settlement departures from the RNV, such as increases in the incidence and severity of wildfires and forest pathogens.

In addition, the proximity of the area to the city of Flagstaff and its popularity as a recreation destination provide an ideal opportunity to educate visitors of the value and qualities of the presettlement forest, as well as of the merits of applying management tools to restore those values and qualities. The fragmentation of the area in terms of management units provides not only a challenge in coordinating efforts between agencies, but also an opportunity to test the feasibility of such coordination of strategies and goals across jurisdictional boundaries.

Oliver et al. (1994) suggested an 8-step systematic approach to achieving forest health. Step 1 was to describe the range of natural variability in order to establish a reference for assessing current forest conditions and desired future conditions. Step 2 was to assess current departures from the range of variability. These two steps represent the focus of the research described here. Oliver et al.'s (1994) remaining steps are: (3) involve scientists, managers, landowners, and the public in determining an acceptable range of variability, using the natural range of variability as a reference; (4) involve all partners in developing management strategies to return the trajectories of forest change within the defined acceptable range of variability; (5) use large areas to demonstrate alternative strategies; (6) use adaptive management strategies, i.e. remain flexible and receptive as new information becomes available; (7) highlight the consequences of alternative management actions; and (8) conduct education and awareness programs, internally and externally. Using Oliver et al.'s (1994) systematic approach as a framework, our research suggests several management strategies aimed at restoring to some extent the presettlement structure and composition of the study area.

First, since frequent, low-intensity forest fires were the most instrumental of the processes which maintained the relatively open, large ponderosa pine-dominated presettlement forest, restoring this process would perhaps be the most accessible management practice towards restoring presettlement forest attributes. Walnut Canyon National Monument already has instituted a prescribed fire program toward this goal. An aggressive prescribed fire program across agency boundaries would be difficult to implement in the area, given its proximity to the Flagstaff urban-wildland interface, local and governmental restrictions, the existence of more high-priority candidate areas for prescribed fire, and the necessity of close interagency cooperation. Nevertheless, recreating some semblance of the presettlement fire regime represents a worthwhile, perhaps an integral, step toward restoring attributes of the presettlement forest.

Other considerations urge caution before a program of frequent, low-intensity prescribed fire is instituted over the entire area. First, it is unknown to what extent a modern prescribed fire would mimic the burn pattern of presettlement fires. Prior to modern fire exclusion, fires were fed by fine fuels, primarily grasses (Cooper 1960). Over a century of livestock grazing in the area likely has reduced the extent and biomass of the herbaceous understory. Without the grassy understory, prescribed fires in the area may not spread sufficiently to achieve the areal extent of presettlement fires. Also, the possibility of larger trees succumbing to fire is greater than it was during the presettlement era, due to over a century of fuel buildup beneath the larger trees. Removal of the duff beneath exceptional trees may be desirable before igniting prescribed fires in the area.

Second, restoring the herbaceous understory is essential towards recreating the presettlement ecosystem structure and maintaining frequent, low-intensity surface fires. The area should be reseeded or planted with native grasses, shrubs, and forbs if natural regeneration is inadequate. Determining the composition and biomass of the herbaceous understory prior to Euro-American settlement was beyond the scope of our research, but it represents a valuable direction for future research in the area (see Fisher et al. [1987] for an example of an approach to this type of research).

Third, excluding herbivores from the area, at least temporarily, may be necessary in order to allow an herbaceous understory to develop which is sufficient to carry frequent, low-intensity surface fires. Livestock use is not heavy in the area, but undomesticated herbivores, especially elk, may consume some or all of the forage made available by excluding livestock. The area is much used by elk (personal observation 1994), probably because most of the study area is within either the Flagstaff city limits or Walnut Canyon National Monument and thus is closed to hunting.

Fourth, although average density in the area has not increased to the extent observed at other locations (Covington and Moore 1994a,b), dense clumps of ponderosa pine and Gambel oak saplings and poles are scattered throughout the area. These clumps are likely to become more common, more dense, and more extensive in the absence of frequent fires. Mechanically thinning these clumps to an approximation of their presettlement densities and occurrences is essential, because prescribed fire alone may be inadequate to restore the presettlement forest structure (Bonnicksen and Stone 1985).

Fifth, restoration treatments will require community support. They also represent an opportunity to educate Flagstaff-area residents and visitors about ponderosa pine ecosystems. Interpretive signs and exhibits, workshops, tours, and other approaches toward raising community interest, knowledge, and support should accompany any program aimed at restoring presettlement attributes in the area.

Sixth, restoration treatments should proceed with increased cooperation across agency jurisdictions. Each of the managing agencies in the area--U.S. Forest Service, U.S. Park Service, and the State of Arizona Land Department--has different missions, management philosophies, and goals. Identifying common goals and incorporating them into a strategy aimed at restoring desirable presettlement attributes over the entire study area would ensure that the largest potential area will benefit from restoration treatments. It also would preclude one agency's activities from interfering with the goals of another; for example, in the event that a prescribed fire on U.S. Forest Service-managed land inadvertently crossed into state-managed land. Other agencies and groups which have an interest in the area, such as the City of Flagstaff, the Friends of Walnut Canyon citizens' group, and adjacent landowners, also should share in developing restoration strategies and goals.

Finally, research into presettlement forest structure, such as that described here, should be accelerated while evidence of presettlement conditions still exists. One of the ironies of presettlement research is that management practices suggested by the research, especially prescribed fire, destroy the stumps, snags, and other evidence which the researcher relies upon to make recommendations. Ultimately, however, over time, virtually all evidence of the nature of presettlement forests will be destroyed. Combining presettlement research with adaptive ecosystem management (Kaufmann et al. 1994) represents the most promising approach towards improving forest health and supplying human needs. Under adaptive ecosystem management, treatments such as prescribed fire are considered experiments: the effects of management treatments represent experimental results which are incorporated into later management efforts. Thus, research is continuous, and strategies are continuously refined in order to manage ecosystems as efficiently and intelligently as is possible. Adaptive ecosystem management, guided by presettlement forest conditions research, will ensure that land managers and the public can work to restore the health of forests to the best of their abilities, while simultaneously furthering our knowledge of ecosystem dynamics.

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The Knowles Cañon Hanging Garden, Glen Canyon National Recreation Area, Five Years after Burning: Vegetation and Soil Biota Patterns

Tim B. Graham[1]

National Biological Service
Cooperative Research Unit
University of California
Davis, California 95616

Abstract. Hanging garden plant communities form at seeps on cliffs. A given community may include common riparian species, disjunct populations, and species endemic to hanging gardens. What structures hanging garden communities, and how they respond to disturbance are poorly understood. In 1989, fireworks ignited a hanging garden in Knowles Cañon, destroying aboveground vegetation. Permanent plots were established in July 1993 to monitor changes in vegetation and soil biota. Revegetation of the garden has been limited to grasses, forbs, and ferns where water was present at the soil surface, and shrubs and trees sprouting from surviving rootstocks. Water drips from the overhanging cliff in the central area, where plant cover is almost 100%. Both moisture and vegetation were patchy along the backwall. The soil was dry in most of the alcove and remained unvegetated 5 years after the fire. Central area soils had more fungus than bacteria and contained mostly root-feeding nematodes. Backwall soils contained more bacteria than fungi, and mostly bacteriovore nematodes. The dry areas had little active bacteria or fungi and few nematodes.

Key words: Colorado Plateau, fire, Glen Canyon NRA, hanging garden, soil bacteria, soil fungi, soil nematodes, succession.

Hanging gardens are mesic plant communities growing on cañon walls on the Colorado Plateau that occur where groundwater seeps laterally out to the cliff surface from perched aquifers (May et al. 1995). Plant communities in hanging gardens range from small monospecific patches of vegetation on vertical cliffs to complex assemblages in large alcoves and can include common riparian species, disjunct populations, Colorado Plateau endemics, and species restricted to the hanging garden environment (Welsh and Toft 1981, Welsh 1989, Fowler et al. 1995).

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[1] Current address: USGS Biological Resources Division, 82 Dogwood Avenue, Moab, Utah 84532.

Natural disturbance of hanging garden communities is limited primarily to rock falls, sloughing of vegetation and colluvium, and herbivory. The crushed or sloughed vegetation is probably replaced by the same suite of species following disturbance (Welsh and Toft 1981). Hanging gardens are often trampled by humans resulting in significant losses of vegetation and soil, and are occasionally burned. Opportunities to study how hanging gardens respond to disturbance can provide guidance to managers in restoration efforts of hanging garden ecosystems.

The Knowles Cañon hanging garden is off the main stem of Knowles Cañon, at an elevation of 1,160 m, in Navajo Sandstone. The garden is two-tiered; the upper terrace consisting of a wide, steeply sloping ledge in a shallow alcove, and the lower section consisting of vegetation on the cliff and around the plunge basin in the cañon floor (Fig. 1).

On 4 July 1989, the Knowles Cañon garden burned from fireworks ignited by visitors. The aboveground vegetation on the upper terrace was completely destroyed, although rootstocks of some species survived. Portions of the lower garden also burned. The fire was very hot, causing rock slabs to spall off the alcove roof. Most of the organic material in the soil of the garden was burned. A few patches of dense litter, mostly leaves and seed pods of *Cercis occidentalis*, or packrat midden material remained.

Species composition of the Knowles Cañon hanging garden was recorded in 1983 (Welsh 1984). This list (see Appendix A) represents the extent of pre-fire knowledge of the hanging garden. Photo points were established and photos taken of the garden in March 1990 by GLCA Resource Management staff. In April 1992 photos were again taken from these photo points.

Post-fire vegetation patterns of the Knowles Cañon garden in 1992 appeared to be driven by two factors: surviving rootstocks and soil moisture. Vegetation was limited to herbaceous species growing in the wettest areas, and sprouting rootstocks of trees and shrubs (primarily *C. occidentalis*, *Quercus gambelii*), and the graminoids, *Phragmites australis* and *Juncus balticus*. There were some desert annuals around the periphery of the garden (e.g., *Eriogonum cernuum*, *Bromus rubens*, and *B. tectorum*). Trees and shrubs showed vigorous regrowth, some were over 2 m tall. Herbaceous species covered approximately 10% of the alcove, but plant cover was 100% in some patches. The rest of the alcove was covered by dry, rocky soil and ash.

Nothing is known about soil communities in hanging gardens, including how changes in soil community structure may affect hanging garden plant succession. Fire generally lowers microbial biomass and respiration, the degree of reduction depends on heat and duration of the fire (Raison and McGarity 1980, Pietikainen and Fritze 1993, Fritze et al. 1993, 1994). Recovery rates also depend on how hot the fire was, amount of ash deposited, and degree of vaporization of soil carbon (Raison 1979, Fritze et al. 1994). Monitoring the soil community in the burned garden over time will provide data on soil community changes. Shifts in plant and soil communities can be

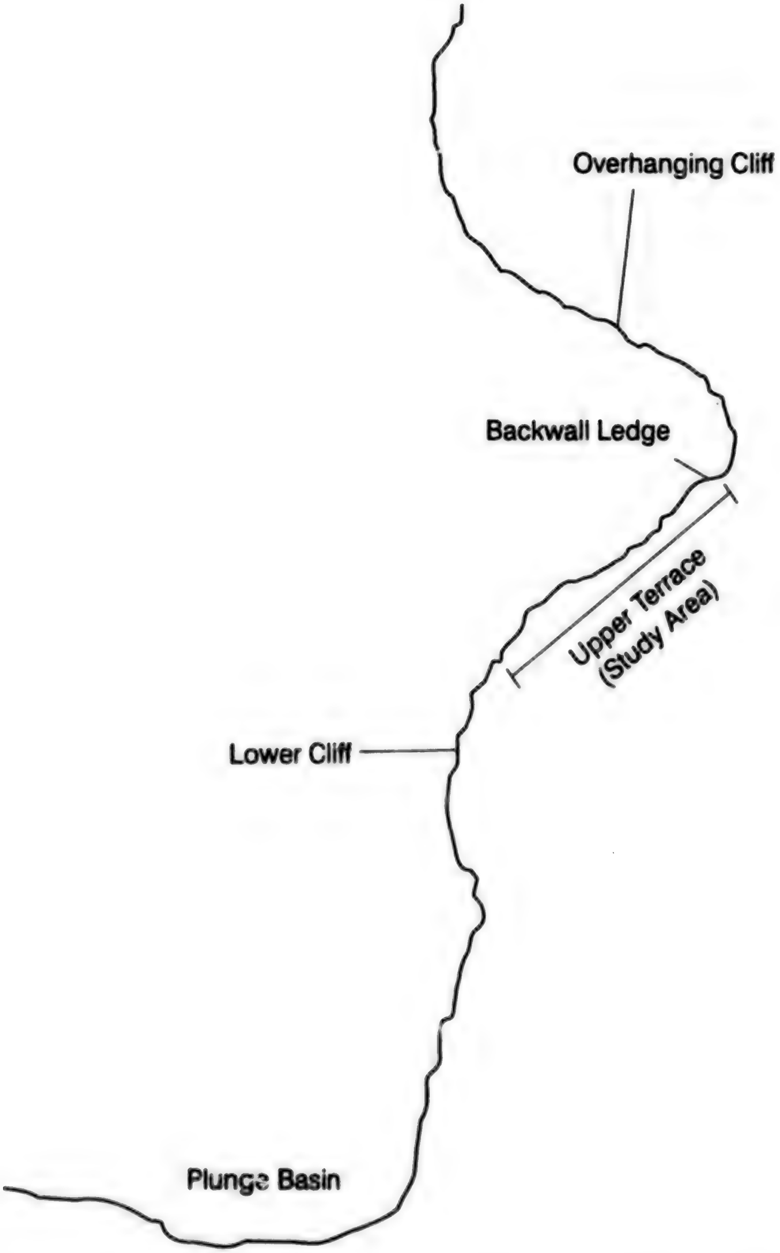

Fig. 1. Schematic drawing of the Knowles Cañon hanging garden, showing a cross-section through the cliff at the alcove and a plan view of the upper terrace.

examined for correlated patterns. Strong correlations may provide guidance for resource managers in more effective protection and restoration of hanging gardens. The fire provided the National Park Service with an opportunity to study successional processes in a hanging garden. This report presents data from the first field season (1993) of a long-term monitoring study of changes in plant and soil communities. The primary goals of the 1993 season were to establish permanent sampling points in the hanging garden, evaluate sampling methods, and establish baseline conditions to compare with future changes.

Study Site

The study was limited to the upper terrace, which burned completely, because access to the lower garden was too difficult. The study area was defined as the colluvial slope within the alcove, between the overhanging cliff and the steep lower slope and cliff (Fig. 1).

The burned upper terrace was divided into four distinct habitats based on location and degree of revegetation (Fig. 2). Different conditions for plant establishment exist in each habitat. The backwall habitat (BW) is restricted to a narrow ledge at the top of the detrital slope and the cliff above it. Water does not run down the cliff uniformly, thus soil moisture along the backwall ledge varies from dry to saturated. The Central Seep habitat (CS) is a fairly small area in the middle of the alcove. It extends from top to bottom of the detrital slope in an area and is defined by wet soils and thick vegetation. The East Dry (ED) habitat is southeast of the central seep and covers the entire colluvial slope from the backwall strip to the lower cliff. It was largely unvegetated, but had *Cercis* growing along the upper and lower boundaries of the dry slope and a patch of *Phragmites* along the eastern edge. The West Dry (WD) habitat is northwest of the central seep and encompasses the detrital slope from the backwall strip to the lower cliff. Like the ED, this area was completely unvegetated in 1993, with *Cercis* and *Brickellia longifolia* along the backwall, and *Cercis*, *Quercus* and *Juncus* along the lower boundary. The ED habitat receives less insolation than the WD habitat, but otherwise the two areas appear to be similar. To facilitate locating random points in the dry areas, I established a permanent 50 m^2 (5 m X 10 m) quadrat in each dry habitat, overlaid a grid on the quadrat, and located 20 permanent plots randomly on each grid. If significant changes occur in other parts of the dry areas, the monitoring can easily be expanded to include those areas. Quadrat locations and transect end points were chosen based on presence of large boulders that would provide relatively permanent markers so plots could be relocated even if the stakes were lost.

Only the narrow ledge of the backwall was sampled because of the difficulties of sampling an overhanging cliff. Plots were located from random numbers along a 30 m transect in the middle of the backwall. All plots are

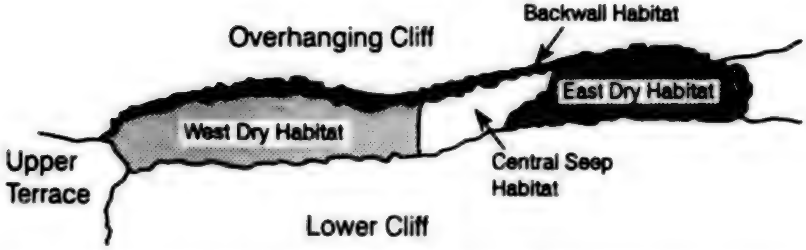

Fig. 2. The upper terrace is shaded to show locations and approximate shapes of the four habitats delineated for this study. the upper terrace shown in plan view corresponds to the upper slope delineated in the cross-section and comprises the entire study area.

permanently marked. Only herbaceous plants were recorded along the backwall. Canopy cover of trees and shrubs was not recorded because of the difficulty in trying to estimate cover above the plots in the confined space of the backwall ledge.

The CS is an irregularly shaped area in the center of the garden with mostly saturated soils, and thick grass or fern cover over most of it. Plots were established along four transects across the garden (two running downslope from the backwall and two traversing the garden roughly along contours). Only the ends of the transects are permanently marked. Plot were located from random numbers along a tape measure stretched between the transect end points.

Methods

A list of all plant species seen in and around the burned hanging garden was made in 1993 as part of a general survey of hanging garden plant community composition in GLCA by John Spence (GLCA unpublished data). Species found on the upper terrace within the defined study area were used as an estimate of the maximum number of species that might occur within each habitat for evaluating the effectiveness of the sampling protocol. Species on the cliff below the terrace, on the overhanging cliff, or found outside the alcove on the terrace were excluded.

Nested frequency (Hironaka 1985, Smith et al. 1987) and percent cover (modified from Daubenmire 1959, see below) for rock, bare ground, litter, and each plant species were estimated in 20 permanent plots in each habitat. Different sized plots were sampled in the four habitats because plant density and total area were different. The dry habitats were sampled with 0.25 m^2 plots (a total of 5 m^2). The central area was sampled with 0.1 m^2 plots (a total of 2 m^2). Twenty 0.05 m^2 plots (1 m^2 total) were sampled in the backwall habitat.

Frequency is the probability of finding a particular species or soil character if a quadrat is placed randomly in an area (Hironaka 1985), and indicates presence/absence within each plot, providing a relative index of abundance. Only plants rooted within the plot frame are considered for frequency. Frequency values are highly dependent on plot frame size as well as plant density and distribution (Hironaka 1985, West 1985). For this reason, a series of nested plots is recommended (Hironaka 1985). Frequency values are calculated by summing the nested frequency scores across the plots for each species then dividing by the number of plots (20), and multiplying by 100. Frequency values using this method range from 0–400.

Plant cover was estimated as the percent of the entire plot frame covered by a species and recorded as a cover class: 1 = <1%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–95%, 7 = 95–100%. Cover was estimated for all plant species occupying space in or above the plot, whether the plant is rooted in the plot or not. Cover of soil characters (e.g., rock, bare ground, etc.) were also estimated using these cover classes.

Percent absolute cover for a species was estimated by multiplying the mid-point of each cover class by the number of plots assigned to that cover class, summing over all cover classes and dividing by the number of plots. Percent cover and frequency were calculated for each species, and for rock, litter, and bare ground in each area. Percent cover for all species was summed to obtain a total plant cover value for each area.

Species-area curves were constructed by plotting the cumulative number of species detected vs. the cumulative area sampled. This was used to evaluate the effectiveness of the sampling design in detecting species present in each habitat (Smith 1974). The number of species that occurred in plots in a habitat was divided by the total number of species observed during plot sampling and the general survey as another measure of sampling effectiveness.

The longest canopy diameter (d_1), and longest diameter (d_2) perpendicular to d_1 were measured for individual *Cercis* to estimate canopy cover of these trees. Trees with overlapping canopies were not measured because of the difficulties of determining canopy boundaries. Canopy cover (CC) was estimated for each tree as: $CC = \pi*[(d_1+d_2)/4]^2$. Canopy cover was summed and average canopy cover per tree calculated.

Twenty soil samples were collected at random points, four each from backwall and central seep habitats, and six from each dry habitat. Each soil sample was a 5 cm diameter core, 15 cm deep, except in the backwall habitat where soil depth ranged from 3 to over 15 cm. Depth of backwall samples were to bedrock, or to 15 cm. Samples were collected 13 July 1993, placed in zip lock bags, and kept on ice until shipped to the Soil Microbial Biomass

Service (SMBS), Oregon State University for analysis. Soil samples were analyzed as described in Ingham et al. (1989) and Coleman et al. (1990). Soil moisture was measured in each sample by subtracting the weight of dry soil from wet soil weight, and is reported as the weight of water that would be associated with one gram of dry soil (g H_2O g^{-1} dry soil). Active bacterial biomass and active and total fungal biomass are reported as µg microbe g^{-1} dry soil. Total nematode numbers and trophic composition of the nematode assemblage were determined, and are reported as # nematodes g^{-1} dry soil.

Results and Discussion

Vegetation

Twenty-three species, and seedlings of an unidentified dicot, were observed in the garden (Table 1). Fourteen species and the dicot seedlings occurred in or over at least one of the 80 permanent plots established (Table 2). The other nine species were uncommon and were often growing on the periphery of the study area. The species list from Welsh (1984) is reproduced in Appendix A. It is not clear from the list which species might have been present on the upper terrace before the fire. Ten of the 24 species Welsh observed in 1983 were present in the upper terrace in 1993 and are marked with an asterisk in Table 1.

The effectiveness of the sampling design varied among habitats. For the whole garden, 62.5% of species seen occurred within one or more sampling plots (15 of 24). Figure 3 shows the accumulation of species detected in sampling vs. the total area sampled (species/area curves) for each of the four habitat patches. The percent of the total number of species observed in each habitat that occurred in sample plots are indicated at the end of each curve. The number of species occurring in plots leveled off in each habitat (Fig. 3), but the curves for the central seep and backwall habitats indicate that additional species might be detected if more plots are examined. The central seep habitat was probably adequately sampled considering that most of the species not detected were rare. More of the backwall should have been sampled and the transect should be extended at both ends for future sampling. In the dry habitats, the low detection rate was a function of the plants occurring around the edges of the habitats and the random plots being located throughout the areas. Additional plots in the dry habitats would monitor a greater total area, which may improve sampling effectiveness as the dry areas begin to be revegetated.

Table 2 presents frequency and cover estimates from plots in each habitat patch. Bare ground and rock covered most of the dry areas. The CS had over 25% of the area unvegetated, and the backwall was almost 50% bare ground or rock. Litter was on the surface in almost every dry plot (frequencies of 380--WD, 395--ED), but except for patches of unburned leaf and seed pod mats,

Table 1. Species observed in the burned portion of the Knowles Cañon hanging garden, 12–13 July 1993, and the habitats in which they were growing. Species present somewhere in the garden in 1983 are marked with an asterisk (Welsh 1984).

Species	Backwall	Center seep	East dry	West dry
*Adiantum capillus-veneris**	x	x		
*Artemisia ludoviciana**			x	
*Brickellia longifolia**	x	x		x
*Bromus rubens**	x	x	x	
Carex aurea		x		
*Cercis occidentalis**	x	x	x	x
*Cirsium rydbergii**	x			
Conyza canadensis		x		
Gnaphalium chilense	x	x		
Juncus balticus	x			
Lobelia cardinalis	x	x		
Mentzelia albicaulis				x
*Mimulus eastwoodiae**	x			
Muhlenbergia andina		x		
Panicum acuminatum	x	x		x
*Phragmites australis**			x	
Polypogon monspeliensis	x	x		
Polypogon semiverticillata	x	x		
*Quercus gambelii**		x		
*Solidago sparsiflora**	x	x		
Sonchus asper		x		
Stephanomeria tenuifolia	x			
Tamarix ramosissima	x	x	x	x
Unknown dicot seedling	x	x		
Total number of species	15	17	7	9

litter was comprised of small leaf pieces. Litter covered less of the BW and CS habitats, largely because living plant material was growing over the litter.

Six species were observed on the east side and were used in species-area calculations (Table 1). *Cercis occidentalis* was rooted along the upper and lower edges of the east dry within the study area and was included in calculating species-area sampling efficiency (Fig. 3), because some trees had

Table 2. Percent cover and frequency estimates of plants and ground characteristics from 20 permanent plots in each habitat (see text for plot sizes in each habitat). Frequency can range between 0 and 400.

Species	Backwall cover	Backwall frequency	Central cover	Central frequency	East dry cover	East dry frequency	West dry cover	West dry frequency
Rock	29.08	230	6.95	125	58.25	385	40.02	395
Bare ground	18.93	205	21.45	175	33.58	310	42.58	385
Litter	13.43	290	10.80	270	21.38	395	28.70	380
Adiantum capillus-veneris	41.28	255	29.63	150				
Artemisia ludoviciana					0.75	20		
Brickellia longifolia			3.88	5				
Bromus rubens			1.50	30				
Carex aurea			3.55	80				
Cercis occidentalis			0.02	15				
Conyza canadensis			0.48	40				
Gnaphalium chilense			0.18	35				
Lobelia cardinalis	0.33	55	0.15	0				
Mentzelia albicaulis					0.15	0		
Muhlenbergia andina			0.15	15				
Panicum acuminatum	0.15	20	2.02	25			0.15	0
Polypogon semiverticillata	0.35	45	28.20	280				
Tamarix ramosissima					4.88	0		
Unknown dicot seedling	0.05	10						
Total vegetation cover	42.16		70.08		5.78		0.15	

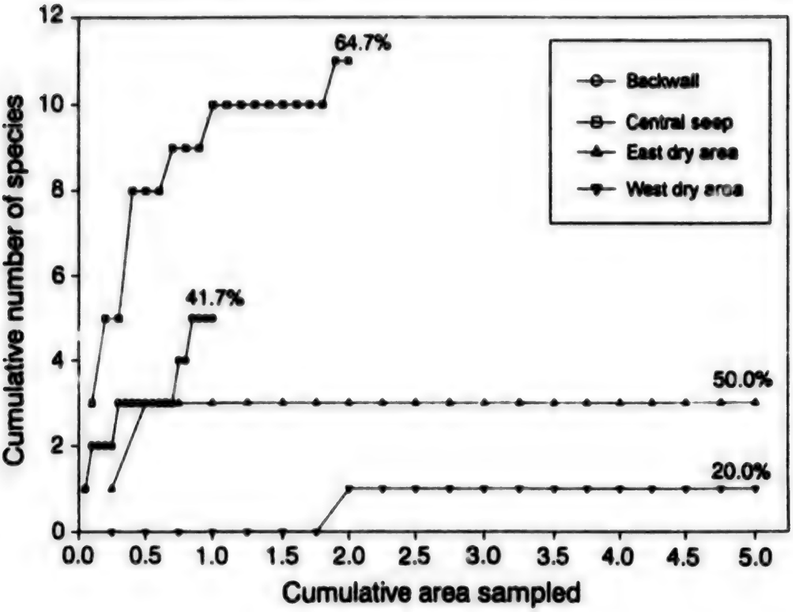

Fig. 3. Species-area curves for each habitat, showing the cumulative number of species with increasing area sampled (= # of plots). Percent of total number of species observed in each habitat that were recorded in sample plots are indicated for each curve.

canopies hanging over the dry area. Three of six possible species occurred in at least one vegetation plot. Total vegetation cover in the east dry area was estimated at 5.8% (Table 2).

Five species were found on the west side and all were located around the edges of the dry area. *Brickellia longifolia*, *Tamarix ramosissima*, and *Panicum acuminatum* occurred along the upper edge of the west study area with at least some canopy hanging over the dry area. *Juncus balticus* was found at the lower edge of the study area. *Cercis occidentalis* was present at both upper and lower edges of the west dry study area. Only one species (*P. acuminatum*) occurring within the defined west dry study area was detected in one of the 20 plots sampled (Fig. 3), and it was rooted outside the plot. Vegetation cover in the 50 m^2 sampling plot was only 0.15% (Table 2).

Sampling along the backwall was designed to monitor only herbaceous vegetation. Tree and shrub species (e.g., *Cercis*, *Brickellia*, and others) were not included in calculating the species-area relationship. Twelve herbaceous species were found along the backwall (Table 1), only five of which occurred in one or more sample plots (Fig. 3). Plants covered only 42.2% of the backwall ledge, and 18.9% of the ledge was bare soil 4 years after the fire (Table 2), even though most of the backwall was moist. Vegetation was dominated by *Adiantum capillus-veneris* (estimated cover 41.3%, 97.9% relative plant cover), and a frequency of 255 (Table 2). The backwall habitat was very heterogenous, as indicated by high species richness and patchy vegetation cover.

The central seep was the most heavily vegetated habitat; total plant cover was estimated to be 70.1%. Much of the area had 100% vegetation and/or litter cover. Seventeen plant species were present (Table 1), 11 of which occurred in plots (Fig. 3). *Adiantum capillus-veneris* (cover 29.6%, frequency 150) and *Polypogon semiverticillata* (cover 28.2%, frequency 280) dominated central seep vegetation (Table 2).

Nine *C. occidentalis* in the west dry area, and eight in the east dry area were measured (about half the trees in each area). Total cover for the 17 trees was 84.5 m^2, average cover per tree was 4.97 $\pm$ 3.67 m^2. The total number of trees was similar in the two areas (19 trees in the west area, 17 trees in the east area), but canopy cover in the WD (61.2 m^2) was much greater than in the ED (23.2 m^2). Average canopy cover was also significantly greater in the west dry area: Mean $CC_{WD} = 6.8 \pm 3.71$ m^2, Mean $CC_{ED} = 2.9 \pm 2.45$ m^2 ($t_{d.f.13} = 2.58$, $P = 0.023$).

Soil Community

Extremely variable soil conditions exist within and between habitats. Table 3 shows soil moisture, active and total fungal biomass, active bacterial biomass, and nematode numbers determined for each soil sample. Variability in soil parameters across the garden make it impossible to generalize about conditions beyond the immediate sample sites.

Soil Moisture

Central seep samples had more moisture than soil from the other three habitats (Table 3). In the BW, the samples above the CS were drier than samples on either side of the central area. Three ED samples and two WD samples were contaminated by water during transit. Soil moisture was not determined for these samples. The contamination of samples with water in transit did not affect estimates of soil biota, only the soil moisture measurements were erroneous (E. Ingham, Director, SMBS, personal communication).

Table 3. Results of soil community analysis for each soil sample in all habitats. Soil moisture is reported as g H_2O g^{-1} dry soil, fungal and bacterial biomass estimates are reported as µg g^{-1} dry soil, and nematodes are reported as number g^{-1} dry soil.

Site	Sample number	Field moisture[a]	Soil H_2O	Active fungal biomass	Total fungal biomass	Active bacterial biomass	Fungal algal biomass ratio	Total number nematodes	Nematode fungivores	Nematode bactivores	Nematode root feeders
Backwall	1	moist	0.24	0.67	37.67	6.42	0.104	0.90	0.33	0.39	0.17
	2	dry	0.06	0.25	46.54	1.94	0.129	0.81	0.05	0.75	0
	3	moist	0.08	0	24.42	1.84	0	0	0	0	0
	4	moist	0.15	4.96	17.86	4.10	1.21	0.28	0.14	0.14	0
Central seep	1	moist	0.56	12.32	74.29	2.32	5.31	5.1	0.14	0.14	1.17
	2	moist	0.61	18.30	132.41	1.91	9.58	0	0	0	0
	3	moist	0.48	31.14	295.74	6.29	4.95	0.18	0.06	0	0.06
	4	moist	1.02	64.86	1591.99	6.52	9.95	0.24	0	0	0.12
East dry	1	dry	b	0.32	1.21	0.06	5.33	0	0	0	0
	2	moist	0.10	0	1.91	0.13	0	0.31	0	0.28	0
	3	dry	b	0	0.59	0	c	0	0	0	0
	4	moist	0.03	4.30	112.20	0.31	13.87	0.16	0.12	0.04	0
	5	dry	b	0	0	0.05	0	0	0	0	0
	6	moist	0.16	14.61	66.59	2.47	5.92	0.05	0	0.04	0
West dry	1	dry	0.01	0	0	0.04	0	0	0	0	0
	2	moist	b	0.76	3.30	0.32	2.38	0	0	0	0
	3	moist	b	0.14	1.33	0.39	0.359	0.08	0	0.08	0
	4	dry	0.01	0	2.63	0.04	0	0	0	0	0
	5	dry	0	0	.46	0	c	0	0	0	0
	6	dry	0.01	0	1.63	0	c	0	0	0	0

[a] Field moisture: indicates whether soil sample was dry or moist when collected.

[b] Samples got wet in transit, soil moisture could not be determined.

[c] No bacteria detected in these samples, thus fungal to bacterial biomass ratios could not be calculated.

Soil Fungal Biomass

Total and active fungal biomass in soils showed the same general pattern of abundance, but total fungal biomass was more variable. Central seep samples had the greatest fungal biomass. Sample ED4, taken in a mat of *Cercis* seed pod and leaf litter, and ED6, taken in the middle of the *Phragmites* patch had very high fungal biomass estimates compared to the other four ED samples. Both were moist at the 10–15 cm depth. The highest fungal biomass value in the west dry area (WD2) also came from a sample taken in seed pod and leaf mat and was moist at 10-15 cm when collected. Active fungal biomass estimates in Knowles Cañon hanging garden soils were lower than levels reported for agricultural soils (91 to 377 μg g^{-1} dry soil, Sakamoto and Oba 1994), but were similar to prairie (0.8 μg g^{-1} dry soil) and meadow (1.2 μg g^{-1} dry soil) soils (Ingham et al. 1989). Ingham et al. (1989) found pine forest soils had higher active fungal biomass (80 μg g^{-1} dry soil) than any Knowles Cañon hanging garden soils.

Soil Bacterial Biomass

Active bacterial biomass was greatest in the central seep habitat, but differences between central and backwall areas were small (Table 3). In both dry habitats samples qualitatively classed as "moist" when collected had the highest active bacterial biomass estimates (Table 3). The backwall and central seep habitats had more bacteria than prairie and meadow soils (1 μg g^{-1} dry soil, Ingham et al. 1989), but less than lodgepole pine forest soils (10 μg g^{-1} dry soil, Ingham et al. 1989), subalpine coniferous forest soils (12 μg g^{-1} dry soil, Bissett and Parkinson 1980), or agricultural soils (82-263 μg g^{-1} dry soil, Sakamoto and Oba (1994).

Active Fungal: Active Bacterial Biomass Ratios

There was a positive relationship between active fungal biomass and active bacterial biomass across the hanging garden ($r^2 = 44.4\%$, $P = 0.0008$; Fig. 4). Three of four backwall soil samples were dominated by bacteria; fungus and bacteria in the fourth sample were similar (Table 3). The backwall area had smaller active fungal:bacterial biomass ratios than meadow, prairie or forest soils reported by Ingham et al. (1989), but differences were relatively small (meadow: 1.2; prairie: 0.8; and backwall: 0.36). In contrast, central seep soils were heavily dominated by fungi (Table 3), resembling pine forest soils (8) studied by Ingham et al. (1989). This is surprising since central seep vegetation was primarily grasses, ferns, and sedges (94% of vegetative cover, Table 2), floristically similar to meadows.

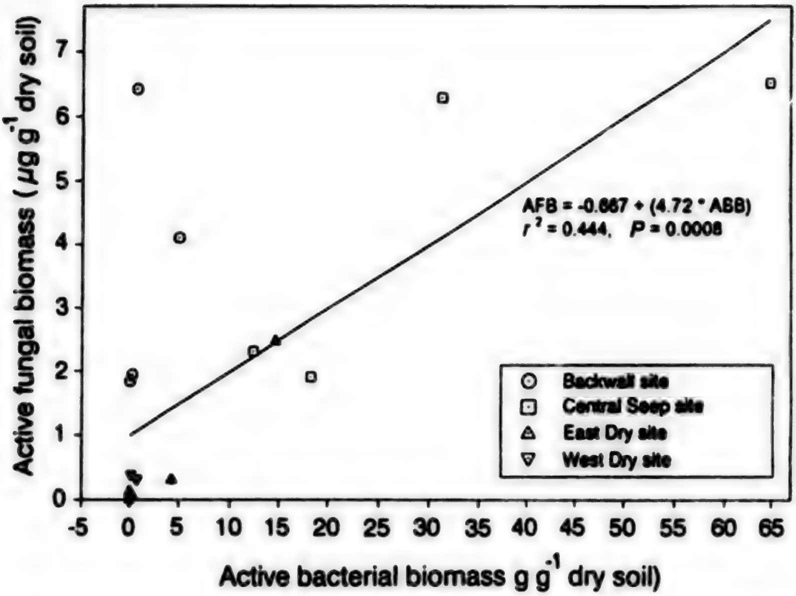

Fig. 4. Active fungal biomass (AFB) plotted against active bacterial biomass (ABB) for 20 soil samples from four study sites within the Knowles Cañon hanging garden. Linear regression line is shown.

Soil Nematodes

Estimated total nematode numbers ranged from 0 to 5.1 g^{-1} of dry soil (Table 3). All four habitats had samples with no nematodes present. The maximum found in each habitat ranged from 0.08 in WD to 5.1 g^{-1} in the central seep. Both the backwall and central seep areas had relatively high numbers. In the two dry habitats, only samples from moist soil had nematodes (Table 3). Both the central seep and backwall habitats had high fungal biomass, yet only the backwall soil contained many fungal-feeding nematodes. More bacteria-feeding nematodes than any other type were found in backwall and dry habitats. The central seep habitat was dominated by root-feeding nematodes.

Conclusions

Plants growing in different parts of the Knowles Cañon hanging garden reflect differences in the environment of each area. Species such as *A. capillus-veneris*, *Cirsium rydbergii* and *Lobelia cardinalis*, found in the central seep and backwall habitats, are typical hanging garden species. A few exotics that regularly invade moist habitats (e.g., *T. ramosissima*, *Polypogon semiverticillata*) were also present. The dry habitats remained largely unvegetated. Even native and introduced annuals (e.g., *Mentzelia albicaulis*, *B. rubens*, *B. tectorum*, *Salsola iberica*) have not become established on the dry sites. Revegetation in these areas has been limited to vegetative regrowth from surviving rootstocks or rhizomes along the upper and lower edges of the dry slope.

Biotic interactions are expected to become more important in the wetter habitats as succession proceeds. The backwall habitat still has large bare areas and plant distribution may reflect the patchiness of soil characteristics such as moisture or soil community composition, differential dispersal or survival of propagules, or some combination of these factors.

Moisture was present 10–15 cm below the surface in parts of the dry habitats. Both *P. australis* and *J. balticus* appear to be exploiting the subsurface water, allowing expansion into the dry habitats. The subsurface water may be capable of supporting plants, but seeds will not germinate until the surface receives water. The burned garden is in an alcove and probably receives little or no direct precipitation. Germination and seedling establishment under these conditions is probably rare. Restoration of disturbed hanging gardens may require transplanting rooted plants that can tap subsurface water as opposed to seeding the area.

There apparently was a trend towards greater microbial biomass with increasing soil moisture in the Knowles Cañon samples, but more intensive sampling is needed to determine whether soil moisture is a critical factor. Other than the abundance of root-feeding nematodes in the central seep, there was little evidence that the soil microbial community was coupled with the overlying plant community in 1993. Patterns in fungal and bacterial biomass and nematode numbers could reflect pre-fire conditions, or represent a reassortment of species following the fire. It is not clear at this time whether there is any relationship between vegetation and soil community successional processes.

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Appendix A. Plant species in the Knowles Cañon hanging garden in 1983 (Welsh 1984).

Plunge Basin

Artemisia ludoviciana
Astragalus lentiginosus
Cercis occidentalis
Baccharis salicina
Rhus trilobata
Brickellia longifolia
Sporobolus reflexa
Bromus tectorum
Cirsium rydbergii
Stephanomeria pauciflora
Bromus rubens
Erigeron bellidiastrum

Face

Epipactis giganteus
Adiantum capillus-veneris

Face (con't)

Mimulus eastwoodiae
Cirsium rydbergii
Solidago sparsiflora
Petrophytum caespitosum
Castilleja linarifolia
Primula specuicola
Lactuca sp.

Detrital Slope

Cercis occidentalis
Phragmites australis
Quercus gambelii
Calamagrostis scopulorum

Physical Resources

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Integration of Grand Canyon Physical and Biological Information: A Progress Report

Vicky J. Meretsky

U.S. Fish and Wildlife Service
P.O. Box 338
Flagstaff, Arizona 86002-0338

Theodore S. Melis

U.S. Geological Survey
1675 W. Anklam Road
Tucson, Arizona 85745

Abstract. Ecosystem management of regulated rivers requires not only integration of different kinds of data, but also effective communication between researchers and managers. We report on recent efforts to improve both processes in lower Colorado River ecosystems of Grand Canyon. Between 1989 and 1995, the Bureau of Reclamation and its cooperators conducted Phase II of the Glen Canyon Environmental Studies to supplement earlier (Phase I) scientific river-based research in Grand Canyon, and produce an environmental impact statement on Glen Canyon Dam operations. Phase II studies were designed to provide "an integrated approach to studying and understanding the relationships between the operations of Glen Canyon Dam and the ecological components of Grand Canyon." By the end of Phase II environmental impact studies, researchers had identified linkages between their own databases and other studies, and opportunities to integrate research were numerous. For example, geomorphology reports contained information relevant to understanding habitat availability for humpback chub. To facilitate integration, the Bureau of Reclamation convened a meeting of Grand Canyon researchers in August 1995. The goal of the meeting was to solicit input on strategies for future integration of abiotic and biotic information. Meeting discussions focused on scientific questions relating to endangered species issues that are best addressed through integrated analyses. Other discussions revolved around the meaning of the term "adaptive management" from a scientific perspective, and the role of science in environmental management. We present an abridged history of past research under the Glen Canyon Environmental Studies program, summarize the results of this first integration meeting, and outline an approach to future integration of physical and biological analyses to improve ecosystem management.

Key words: Adaptive management, biological opinion, ecosystem management, environmental impact statement, integrated management.

Summary History of the Glen Canyon Environmental Studies

Use of integrated scientific information in the management of regulated river ecosystems has been identified as a key to preserving freshwater resources and maintaining biodiversity in rivers (Naiman et al. 1995, Stanford et al. 1996). Currently, an integration effort is underway on the Lower Colorado River within Grand Canyon National Park, Arizona. This effort is a result of previous research surrounding operation of Glen Canyon Dam. To provide a perspective on the current state of scientific integration on the Colorado River in Grand Canyon, we begin with a brief summary history of the Glen Canyon Environmental Studies. No review of this limited scope can do justice to the complexities of many years of political and scientific history; we intend merely to sketch the relevant background that provides some perspective on present integration efforts.

Overview of Phase I Studies

The Glen Canyon Environmental Studies were initiated by the Bureau of Reclamation in 1982 to further investigate relationships between Glen Canyon Dam operations and changes in Colorado River resources throughout Grand Canyon (Dolan et al. 1974, Laursen et al. 1976, Turner and Karpiscak 1980, Howard and Dolan 1981). Although some effects of flow regulation were relatively obvious by that time, many other cause-and-effect relationships and ecosystem links between Glen Canyon Dam operations and the downstream river environment were still uncertain some 20 years after closure of the dam in 1963.

Phase I studies involved federal and state research primarily from 1983 to 1986, with some studies and summary efforts extending to 1988. The program included descriptive studies of aquatic and terrestrial biology, avifauna, sediment-transport processes, hydrology, and recreational use. The results of Phase I research were presented as a series of single-discipline technical reports and publications (U.S. Department of the Interior 1988a,b). These studies confirmed that dam operations affected downstream resources. However, reservoir spills from 1983 through 1986 limited scientific understanding of effects from fluctuating flows resulting from typical hydropower operations – the primary focus of the original research.

Following their review, the National Research Council commented that despite extensive research during Phase I, the resulting single-discipline reports lacked integration, particularly in the planning phase (National Research Council 1987). Information from the different disciplines had not been linked, and the resulting understanding of the system was therefore less complete than it could have been had the studies been integrated from the start. For example, information on hydrology and organic material in the water column had not been brought together with information on humpback chub diet to examine food availability over time and space. To provide deeper insight into the implications of initial research, documentation was prepared to summarize the results and conclusions of Phase I research (U.S. Department of the Interior 1988b).

The National Research Council concluded that the Glen Canyon Environmental Studies had met the overall goals and objectives, and demonstrated that impacts on Grand Canyon related to Glen Canyon Dam operations could be reduced (National Research Council 1987). The Council also noted that the effectiveness of Phase I would have been enhanced by early, rather than after-the-fact, involvement of an integration group, and by greater use of historical data from Grand Canyon and external literature derived from similar fluvial systems. In 1988, the Department of the Interior concluded that additional technical information was needed before dam operations could be modified in order to minimize impacts on downstream resources. Phase II studies were implemented to meet this objective.

Overview of Phase II Studies

Phase II studies began in 1988. At the recommendation of the National Research Council, a senior scientist was appointed to provide direction and oversight for the overall study plan (Patten 1991). Shortly after Phase II studies began, the Department of the Interior mandated an environmental impact statement on the operation of Glen Canyon Dam. The goals and schedule of Phase II studies were modified and accelerated to support the environmental impact statement process. This redirection of Phase II studies eliminated aspects of integration that had originally been planned, in favor of rapid evaluation of areas of special concern for the environmental impact studies.

Phase I reports, available Phase II draft reports, and additional information solicited from scientists were used to: (1) design and implement research flows during the first year of Phase II (1990); (2) implement "interim" flows following cessation of research flows (beginning in August, 1991); and (3) evaluate seven proposed operating alternatives for the Environmental Impact Statement (1990–1995; U.S. Department of the Interior 1995). Interim flow releases were set at 8,000–20,000 cfs to minimize impacts to downstream resources. Interim flows, implemented as part of the annual operating plan for the Lower Colorado River, continued at least until a Record of Decision finalizing the impact statement process was signed by the Secretary of the Interior in October 1996 (the time of completion of this manuscript).

Phase II studies investigated many ecosystem-level responses to dam operation between Glen Canyon Dam and Lake Mead, including research on tributary-process effects, mainstem sediment transport, hydrology, water quality, limnology, geomorphology, aquatic resources, native and endangered species, recreational uses, cultural resources, and economics related to Glen Canyon Dam operations (U.S. Department of the Interior 1995). The relationships among these diverse areas were formalized in a diagram (Patten 1991) that is still undergoing development (John C. Schmidt, personal communication). Although the intent of Phase II research was to promote an integrated approach, as a result of the EIS process. Phase II focused on individual disciplines and research needed before integration could be accomplished. Thus, despite being centrally coordinated through the Bureau of Reclamation's Glen Canyon Environmental Studies office, most Phase II research reports completed in 1995 still required an expanded degree of scientific and technical integration to provide managers with comprehensive information relating river resources to dam operations (National Research Council 1996). Additional integration efforts are underway to integrate various aspects of fisheries research and, separately, sediment-related research.

The Ad-Hoc Interdisciplinary Integration Work Group

As Phase II studies concluded and final reports were submitted, the Glen Canyon Environmental Studies office and its cooperators faced the task of consolidating the scientific information available. More information was available from existing databases than was presented in existing reports, and critical linkages and relationships between river resources and Glen Canyon Dam operations were not fully described by the largely single-discipline reports and publications. It was recognized that additional information might be obtained through interdisciplinary debate, data sharing, and ongoing discussion. To this end, the Glen Canyon Environmental Studies office invited a group of researchers with ongoing ties to the Grand Canyon to discuss possible approaches to integrating existing data.

The Ad-Hoc Interdisciplinary Integration Work Group (hereafter Ad-Hoc Working Group) provided a forum for scientific integration of Lower Colorado River data related to ongoing management needs, particularly those related to Biological Opinion issues. In late 1995, a research center recommended by the Glen Canyon Dam Operations Environmental Impact Statement (U.S. Department of the Interior 1995), was approved, although its full operation is not anticipated until 1997. The Grand Canyon Monitoring and Research Center is intended to take the responsibility of directing long-term monitoring and research of resources below Glen Canyon Dam. In the last months of 1996, the Center began contacting Grand Canyon researchers to continue the process begun by the Ad-Hoc Working Group.

The first meeting of the Ad-Hoc Working Group was convened in August 1995, and was comprised of representatives from federal and state agencies, academia, the private sector, and Native American tribes. Researchers who could not be present were and continue to be encouraged to participate in the integration process as opportunities and interests arise. To better focus discussions on science, three topics were accepted by the group for further exploration and debate: (1) physical-habitat relations (divided into geomorphology/sedimentology and hydroclimatology subcomponents); (2) trophic dynamics; and (3) population ecology of humpback chub (divided into subcomponents of life-history strategies and species interactions). In addition, the group recognized a strong need to discuss the role of science and scientists in the adaptive-management process. Thus, an additional section (4), on adaptive management and its relation to science and scientists was added to the core topics.

Evaluating Approaches to Science Integration

Core-topic discussions concluded with the formation of writing groups. From August through November 1995, principal topic authors presented integration documents to their respective groups, received and incorporated comments, and completed draft integration prospectus modules. The resulting core-topic integration reports were brought together with introductory and background information and presented as an informal, but comprehensive draft prospectus to the research community (Ad-Hoc Interdisciplinary Integration Work Group 1995). The following sections summarize the main points of the integration prospectus and discuss future integration goals of that process.

Physical-Habitat Relations – Geomorphology, Sedimentology, and Hydroclimatology

Environmental studies of the effects of Glen Canyon Dam operations on downstream river resources indicate that physical attributes of habitats are controlling factors in the ecology of many species in Grand Canyon (U.S. Department of the Interior 1995). Other controlling factors include food availability, river temperature, and biotic interactions. Most Colorado River researchers attending the August 1995 Fern Mountain meeting agreed that integration of existing biotic and abiotic data bases generated during Phases I and II of the Glen Canyon Environmental Studies would lead to the development of specific, testable hypotheses regarding these habitat relationships. For example, relationships between life histories of native fish, decade-scale climate variability, and mainstem and tributary geomorphology might be explored through such hypotheses. The group also recognized that scientists and managers working together towards integration of scientific data will be better able to manage endangered/critical species by managing operations at Glen Canyon Dam, but only after specific relations between habitat and species distributions are understood.

The following section outlines discussions that occurred during the meeting with regard to the potential significance of incorporating physical data into Biological Opinion related research on the Lower Colorado River. Owing to the dynamic nature of Grand Canyon's climate and geomorphic processes, the habitats of endangered species change naturally through time, but these changes have also been influenced by regulated dam releases since 1963. Physical changes in the river's geomorphic framework are linked to regional geologic characteristics and climatic variability. Significant geomorphic changes in the mainstem Colorado River below Glen Canyon Dam have been recently documented (Schmidt and Graf 1990, Webb et al. 1991, Melis and Webb 1993, Melis et al. 1994, McGuinn-Robbins 1995, Melis et al. 1995, Schmidt and Rubin 1995, Stevens and Wegner 1995, Stevens et al. 1995, Webb and Melis 1995, Webb 1996, Webb et al. 1996). These changes will likely continue as a result of natural and man-caused disturbances resulting from unregulated geomorphic processes in Grand Canyon (e.g., floods, rock-falls, and debris flows), and dam operations (e.g., suppression of flooding, unplanned reservoir spills, prescribed experimental floods, and thermal effects from selective-withdrawal implementation). The next step towards understanding the subtle implications of these changes on the physical resources and aquatic ecosystem below Glen Canyon Dam is a comprehensive integration of existing data and conclusions derived from past studies.

The hydroclimatology of the Colorado Plateau affects a variety of physical and biological processes in Grand Canyon related to critical species' ecology. Flows in the Colorado River upstream from Lake Powell, the Little Colorado River, and other tributaries in Grand Canyon respond to topography in concert with regional climate variability that is driven by global-scale processes. Global processes include general circulation patterns in the atmosphere, and Pacific Ocean sea-surface temperatures and currents (Rasmusson and Carpenter 1982, Liu et al. 1995). Anomalous circulation in the atmosphere and the global-scale phenomenon of El Niño (Diaz and Markgraf 1992) in the eastern Pacific Ocean affect climate and weather on the Colorado Plateau (Andrade and Sellers 1988, Cayan and Webb 1992), as well as the rest of the western United States (Redmond and Koch 1991, Kahya and Dracup 1993). In addition, recent studies suggest that daily precipitation intensities have increased during the twentieth century throughout the United States (Karl et al. 1995), a trend which has potential significant geomorphic implications on river systems such as the Colorado River Basin.

Another first step toward understanding the significance of habitat changes along the Colorado River is integration of biotic life-history data for critical species. These data include demography, distribution, behavior, relations to associated species, reproduction, and habitat requirements. Once data on the geomorphology of the river and species ecology are individually integrated, life-history models may be linked to physical-habitat information. Abiotic data likewise require synthesis for integration to succeed, including basin-to-macro scale characteristics controlling the geomorphic framework of the Colorado River, tributary/river process interactions, relations of pre- and post-regulated hydrology to river resources, macro-to-micro scale characteristics of the river channel, its canyons and tributaries, present climate effects of regulation on the river, relations of paleohydrology and paleoclimatology to the present geomorphic framework of the system, and models of sediment transport and hydraulics. Developing links between abiotic and biotic systems is a difficult task, but the Ad-Hoc Working Group concluded that such a task can be accomplished through ongoing scientific integration and interdisciplinary research designs that are supported during long-term monitoring.

At present, relationships between the geomorphic framework of the Colorado River, including its hydrology, geology and sedimentology, and its aquatic and riverine habitats, are only generally understood despite considerable research efforts aimed at understanding the individual components of the river system. For example, Valdez and Ryel (1995) hypothesized that a distinct, grouped distribution of humpback chub aggregations in Grand Canyon occurs because of a unique combination of temperature and physical habitat parameters, along with specific life-history requirements for both adult and subadult life stages. Also, Stevens et al. (1995) documented spatial scale impacts of geomorphology and dam operations on marsh development. Predictions of impacts of higher flows on these habitats and assemblages require testing.

Scientists who participated in the August 1995 integration meeting at Fern Mountain, Arizona developed questions designed to begin investigating the links between habitat and endangered species distributions below Glen Canyon Dam. Primary questions posed regarding habitat relationships included: (1) which physical and geomorphic attributes of the Colorado River limit or control distributions of endangered species below Glen Canyon Dam; and (2) how do long/short-term dam operations affect those physical/geomorphic attributes, and how do these effects relate to management objectives for preserving critical species? Neither of these questions can be answered solely by assembling and interpreting existing data bases. However, the timely integration of such information is an essential next step towards an ecosystem-science approach aimed at addressing Biological Opinion issues (U.S. Fish and Wildlife Service 1994).

Additional research on relationships between climate, Lower Colorado River flows, and unregulated tributary processes will provide greater insight into the importance of physical habitat changes and relationships to critical species and ecosystem responses. Besides several integrated research topics on sediment transport and the other natural processes controlling the geomorphic framework of the river, other topics were suggested by the Ad-Hoc Working Group that focus on climate related issues:

- relations between climatic non-stationarity and basin hydrology (Graf et al. 1991);
- climate forecasting related to reservoir and dam operations (Pulwarty and Redmond 1997);
- climate-driven tributary processes and their influence on mainstem habitats (Webb et al. 1991, Melis et al. 1995, 1996, Stevens et al. in press);
- climate's role in the Colorado River basin's long- and short-term sediment balance (Hereford and Webb 1992);
- climatic forcing of the river's bottom-up ecosystem, including the food base (Grimm 1993);
- modeling climate variability effects on water resources (Leavesley 1994);
- the role of localized weather and micro-climate at river level (Marcus et al. 1996).

Another step towards integration of abiotic and biotic information includes designing long-term monitoring so that the above questions can be formulated as focused, management-driven hypotheses and be tested. This task was started in 1996 by the Grand Canyon Monitoring and Research Center staff as part of developing the long-term monitoring and research plan. The questions listed above might ultimately be answered through a wide range of experimental and historical studies that successfully link documented relationships of species' distributions and ecology with physical habitat, water quality, and biotic factors such as aquatic productivity and population dynamics. Such a complex ecosystem approach to this science/management challenge can succeed only through continued institutional support of innovative, interdisciplinary efforts by a diverse group of scientists and decision makers. The potential success of this approach in turn relies on a commitment by decision makers to pursue holistic management of resources through integrated scientific research, with integration implemented from the proposal development phase on through to final report completion. The objective of this prospectus development process was to identify critical habitat hypotheses that required testing. With this integration, decision makers will be better informed as they prioritize resources, direct ongoing research, and achieve management objectives in the future.

Trophic Dynamics

Phase II studies addressing trophic dynamics included research on sediment transport (Schmidt and Graf 1990, Andrews 1991, Cluer 1991, Cluer and Carpenter 1993, Schmidt 1993, Schmidt and Rubin 1995), organic drift (Angradi and Kubly 1994, Ayers and McKinney 1995), benthic ecology (Czarnecki and Blinn 1978, Blinn et al. 1994, Shannon et al. 1994, Stevens et al. in press), photosynthetically available radiation (Yard et al. 1993, Bureau of Reclamation, unpublished data), water quality studies in Lake Powell (Stanford and Ward 1991, Ayers and McKinney 1996, Vernieu 1996, Bureau of Reclamation, unpublished data, U.S. Geological Survey, unpublished data), primary and secondary production (Blinn and Cole 1991, Hardwick et al. 1992, Angradi and Kubly 1993, Ayers and McKinney 1995, 1996), diet of humpback chub (Carothers and Minckley 1981, Kaeding and Zimmerman 1983, Maddux et al. 1987, Kubly 1990), and overview studies (Carothers and Minckley 1981, Maddux et al. 1987, Angradi et al. 1992, Blinn et al. 1994, 1995, Angradi 1994). The Ad-Hoc Working Group suggested that synthesis in this area should be aimed towards the development of large-scale models that relate dam operations and physical factors to food web interactions and population dynamics of species of concern. The following were suggested as a non-exhaustive list of major topics:

- nutrient and other chemical dynamics in Lake Powell,
- light limitations on riverine production over time,
- the role of temperature on river assemblages and food web interactions,
- tributary and mainstream nutrient dynamics and spiraling,
- the role of different size fractions of drift,
- reservoir and riverine decompositional and microbial processes,
- basic life histories and requirements of cornerstone species (e.g., *Oscillatoria* and *Simulium*),
- the role of spatial scale in geomorphology controlling aquatic food base development,
- the role of climate and climatic variability in aquatic food base development, and
- food web and ecological linkage between aquatic and riparian domains.

These topics do not have equal value to managers, and management input would be needed to prioritize/modify the list. In the long term, overall ecosystem models would be useful to predict effects of dam operations.

Key areas of information needed to address these topics included potential production; resource availability; invertebrate, fish, and riparian fauna diets; habitat development and distributions; ecosystem linkages; and management considerations. Selected research hypotheses were also generated, with assessments of existing data and syntheses required.

Population Ecology of Grand Canyon Humpback Chub

Life History Strategies

The Grand Canyon and its tributaries currently support only one viable population of the four endangered big-river fish species: the humpback chub (*Gila cypha*). For this reason, the status of the humpback chub is of major concern, and many dam operations are potentially constrained by their impact on the chub. Data on this species have been collected from the Upper Colorado River Basin above Lake Powell (Valdez and Clemmer 1982, Valdez et al. 1990, Kaeding et al. 1990, Karp and Tyus 1990), from the mainstem Colorado in Grand Canyon (Kaeding and Zimmerman 1983, Valdez and Ryel 1995, 1996), and from the Little Colorado River (Kaeding and Zimmerman 1983, Minckley 1992, Gorman et al. 1994, 1996, Douglas and Marsh 1996, Meretsky et al. 1996). To date, these data have not been integrated. Efforts are needed to combine demographic, distribution, movement and diet information in order to develop a conceptual life-history model for the species, along with information on how life history varies among populations. Such a model will indicate the range of physical conditions chub can tolerate, and identify factors which potentially limit growth and reproduction. Many researchers believe much of this model can be constructed using existing data.

Interactions Between Native and Nonnative Fish

Dam operations differentially affect fish species, and the present understanding of effects of dam operations on interactions between native and nonnative fish species, and between fish species and disease and parasite organisms (Carothers et al. 1981, Valdez et al. 1982, Minckley 1991, Minckley and Deacon 1991, Angradi et al. 1992), is limited. Thus, it is difficult to predict impacts of actions such as high flows or modifications to water temperature regimes.

Four primary questions were identified by the Fern Mountain work group:

1. What are the present effects of fish species interactions in Grand Canyon?

2. What are the important species that interact with native fishes and are these interactions negative, neutral, or positive?

3. How will future management actions related to dam operations affect these interactions?

4. Do fish interactions result in increased levels of parasites or pathogens in native fish?

Grand Canyon fisheries researchers stated that some existing research, especially from outside Grand Canyon, will help answer these questions, but many aspects of the questions had not yet been addressed.

The Role of Science and Scientists in Adaptive Management

Three different laws define decision making for Glen Canyon Dam operations. The preferred alternative of the Operation of Glen Canyon Dam Environmental Impact Statement (environmental impact statements are mandated by the National Environmental Policy Act of 1970) relies on adaptive management (U.S. Department of the Interior 1995:36) to ensure that dam operations comply with the Endangered Species Act of 1973, as defined by a Biological Opinion from the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service 1994). The Grand Canyon Protection Act of 1992 is intended to restore and preserve resources downstream of Glen Canyon Dam, and to see that science is linked to management so that the concerns of all parties interested in Glen Canyon Dam operations and resources are considered. Well-informed decisions will rely not only on timely integration of existing information, but also on effective communication of scientific knowledge to managers and other decision makers (stakeholders).

The Ad-Hoc Working Group maintained that in addition to the scientific integration topics, the role of science and the level of participation by scientists in the planned Grand Canyon adaptive management process needs to be better defined. On the basis of the consensus that the adaptive management process has been extensively described in literature (Holling 1978, Walters 1986, Lee 1993, Wegner 1995, Gunderson et al. 1995), but is inherently open to many misunderstandings and difficulties (Marzolf 1991), Ad-Hoc Working Group scientists agreed to outline a separate prospectus on that topic. It was decided that a position statement on the role of technical scientific support in assisting the future Glen Canyon Dam Adaptive Management Work Group might be useful to both scientists and decision makers as the adaptive management process begins. At the time of manuscript preparation, this group was anticipated to become a Federal Advisory Committee sometime during 1997. The adaptive management group would be composed of basin-wide stakeholders who would evaluate relationships between future operations of Glen Canyon Dam on downstream resources. Based on science and management objectives, this adaptive management advisory committee is intended to make recommendations directly to the Secretary of the Interior (or designee) on whether operations should be modified to ensure protection of downstream resources (U.S. Department of the Interior 1995:36). The adaptive-management discussion group at Fern Mountain explored ways to ensure that the results of basic science and its interdisciplinary integration would be communicated to managers, and that such information would be used in decision making. In addition, discussion group participants emphasized the need for management concerns and objectives to be effectively communicated to scientists in a manner that permitted prioritizing research efforts. Integration can improve understanding of the Grand Canyon ecosystem, but without adequate communication between researchers and other stakeholders, integrated scientific information cannot fully benefit decision making.

Discussion-group participants recognized the principles guiding the design and intent of the adaptive management program and process, as outlined in the Operation of Glen Canyon Dam Environmental Impact Statement, including:

- A long-term monitoring and research program that is designed by qualified researchers in direct response to the needs and objectives defined by management agencies.

- A process that coordinates and communicates management agency needs to researchers and that develops specific recommendations for decision making,

- A forum that effectively transfers monitoring and research findings to the management agencies, and that results in consensus on management responses to information on affected resource conditions, trends, processes, and prioritization of actions.

- Monitoring and research programs in Glen and Grand Canyons that are independently reviewed.

- A forum for all interested parties that allows opportunities for participation in proposals and recommendations that result from adaptive management (U.S. Department of the Interior 1995).

The Ad-Hoc Working Group strongly agreed that the principles stated above require that management, maintenance, prioritization, and integration of diverse information found in varied data bases be pursued, in concert with clear mechanisms for resolving disputes.

In general, the Ad Hoc Working Group recognized that many management related questions could be answered through integration of existing and future scientific data if a holistic and open approach was supported. Although many Lower Colorado River research issues are complex, most participants believed that solutions to many Biological Opinion challenges were possible through ongoing, integrated monitoring and research. The group also agreed that integrated results from Colorado River monitoring and research below Glen Canyon Dam must be communicated to decisionmakers in timely, clear and concise ways that address specific management objective issues directly. For this communication process to occur, management questions and objectives must be clearly stated to managers and researchers well before studies are planned and implemented, so that management objectives are specifically addressed by long-term monitoring and research. Meeting this objective is one of the primary duties of the Grand Canyon Monitoring and Research Center's Chief Scientist. In 1995, management objectives were drafted by a working sub-group of stakeholders, and reviewed by the interim Adaptive Management Working Group (known informally as the Transition Work Group until designated as a Federal Advisory Committee). The draft management objectives were used extensively in 1996 by the Grand Canyon Monitoring and Research Center Chief and his planning group to develop a draft long-term plan for monitoring and research of river resources below Glen Canyon Dam. This plan was scheduled for full implementation in October of 1997 through a variety of competitive proposal requests and interagency agreements (L. D. Garrett, personal communication, 1996).

The Operation of Glen Canyon Dam Environmental Impact Statement recommends that an adaptive management process be implemented to facilitate a management-directed discourse between scientists, decision makers, and all other interested parties (U.S. Department of the Interior 1995:34–37). The Ad-Hoc Working Group was very supportive of this approach. The group thought that general questions such as "How has mainstem fish habitat structure changed since closure of Glen Canyon Dam?" might provide insights to managers on Biological Opinion related issues. This question could be answered by physical scientists using existing databases, and results could be used to pose more complicated hypotheses about how such changes have influenced population dynamics of native and nonnative fishes, in light of documented dam operations. However, questions such as this one may need to be more tightly focused if research results are to be applied; adaptive management would provide a useful arena for the process of focusing objectives. The Chief Scientist of the Grand Canyon Monitoring and Research Center undertook the task of developing a long-term monitoring and research plan in winter 1996 within an open process with help from involved scientists and stakeholders.

Fern Mountain meeting participants emphasized that synthesis of reach-by-reach comparisons of geomorphic data, such as reach-varied debris-flow frequency and magnitude (Melis et al. 1994, 1995), channel/eddy characteristics (Schmidt and Graf 1990), backwater habitats (McGuinn-Robbins 1995, Stevens et al. 1995), shoreline-type distributions (Valdez and Ryel 1995), etc. would eventually be required by Biological Opinion researchers. The timeliness of physical and biotic data integration was deemed important, because experiments requiring that information were being planned at the time of the meeting (e.g., experimental beach/habitat-building test flow, implemented in spring 1996). Incorporation of integrated physical data into conceptual ecologic models for species of interest was a stated priority, as well as a comprehensive synthesis of biotic data. The Ad-

Hoc Working Group also recognized that opportunities to learn are presented by both anticipated and "surprise" outcomes resulting from management decisions and implementation of new conservation measures, including large-scale experiments (Walters and Holling 1990).

Summary

The Ad-Hoc Working Group concluded that whenever integration questions and results are obtained, they must be reported in a timely manner so that decision makers have abundant opportunities to incorporate new physical system information into management strategies aimed at Biological Opinion issues. Addressing as many relevant research and management issues as possible will allow interdisciplinary scientists to better understand what is and is not known about the physical controls of the river's ecosystem, and how such information is relevant to resource management objectives. Only then can integrated biotic models be coupled with the geomorphic framework of the river, and climatic processes in ways that are meaningful for decision makers. The Ad-Hoc Working Group also recognized that opportunities to learn are presented by both anticipated and "surprise" outcomes resulting from management decisions and implementation of new conservation measures, including large-scale experiments (Walters and Holling 1990). Several predicted and surprise results occurred from the 1996 Glen Canyon Dam Beach/Habitat-Building Test Flow. The Ad-Hoc Working Group expressed support for the timely incorporation of those experimental results into the long-term monitoring and research plan design.

Successful scientific integration depends on establishment of links between existing biotic/abiotic databases, an inherently difficult task requiring coordination, ongoing support, multi-disciplinary scientific debate, and flexibility in developing ongoing interdisciplinary research strategies. The Ad-Hoc Working Group also recognized the importance of continually adding to the existing knowledge of river hydrology and sedimentology, because water and sediment together form the river ecosystem's physical framework; this will occur through long-term monitoring and research. Meeting participants advocated that future geomorphic research and monitoring efforts should be designed and coordinated in ways that allow questions to be scientifically examined and tested by methods that cross discipline boundaries, a process that requires open communication among researchers and stakeholders. As stakeholders and scientists work together to continue establishing and prioritizing resource preservation and restoration objectives, many links between species ecology, habitat, and climate will likely arise. Many new developments in management of the Lower Colorado River ecosystem likely will be difficult to anticipate. If an integrated science program is in place when unforeseen issues arise, these unanticipated developments can be addressed more efficiently. In the future, it will be important to promote and nurture new types of working relationships, modes of communication, and methods of coordinating interdisciplinary studies, and these strategies may be difficult to implement initially. However, with the 1995 development of a draft integration prospectus focused on Biological Opinion issues, the Glen Canyon Environmental Studies office took an important step required to achieve true scientific integration.

Aftermath

Shortly after the Fern Mountain meeting, the Glen Canyon Environmental Studies office received permission to conduct a habitat-building test flow – an experimental flood – in Grand Canyon. The exercise involved over 100 scientists in a tightly-focused, logistically complex set of experiments. Because of the earlier integration work, most of the researchers were now familiar with each others' research; much potential redundancy was eliminated, and planning was streamlined. In the months after the experimental flood, cross-discipline partnerships have persisted, and several integrative papers are in progress that would not have been considered before the Fern Mountain meeting. We hope that opportunities for such collaboration will continue as oversight of Grand Canyon research moves from the Glen Canyon Environmental Studies office to the Grand Canyon Monitoring and Research Center.

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Evidence for Deep Water Deposition of the Tapeats Sandstone, Grand Canyon, Arizona

Elaine G. Kennedy
Ray Kablanow[1]
Arthur V. Chadwick[2]

Geoscience Research Institute
Loma Linda University
Loma Linda, California 92350

Abstract. The Tapeats Sandstone forms the basal Cambrian deposit of the Tonto Group and is generally interpreted as a shallow marine deposit. In the Grand Canyon, the sandstone was deposited on a low-relief pre-Cambrian surface broken by scattered remnant cliffs of Shinumo Quartzite and isolated granitic hills. Paleoslope measurements and sedimentological features were recorded at 63 sections from 21 localities in the Grand Canyon exhibiting significant pre-Cambrian topographic relief. At 24 of these sites, debris flows were apparently initiated by some catastrophic event that simultaneously broke and transported Shinumo clasts in a matrix of Tapeats Sandstone. These brecciated flows were deposited along the pre-Cambrian surface topography from the cliff-faces basinward. Widespread preservation of the breccias along topographic relief during the deposition of the entire thickness of Tapeats Sandstone and much of the overlying Bright Angel Shale indicates that deposition of even the shallowest material was below storm wave base. Thorium/uranium (Th/U) ratios from the breccia matrix in Ninety-one Mile Canyon indicate sediment deposition in a reducing environment. Such conditions are unlikely in a high-energy, nearshore facies. These submarine flows were deposited on a surface with over 140 m of vertical relief and would have required water depths in excess of 200 m below storm wave base. Sedimentary structures used to identify the Tapeats Sandstone as a shallow water marine facies need to be reevaluated. To explain the features documented in this research, we propose that the Tapeats Sandstone was deposited as a deep-water, submarine fan complex.

Key words: Breccia, Cambrian, deep water, monadnocks, Ninety-one Mile Canyon, Shinumo quartzite, trace elements.

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[1] Geological Technics, Inc., 2741 River Road, Modesto, California 95351.

[2] Southwestern Adventist University, Keene, Texas 76059.

The Tapeats Sandstone crops out in the Grand Canyon and elsewhere in Central Arizona and forms the basal Cambrian deposit of the Tonto Group (Beus and Morales 1990). Various authors have postulated shallow marine as well as subaerial origins for the Tapeats Sandstone and other basal Cambrian deposits of the Western United States, based on detailed facies reconstructions (McKee and Resser 1945, Wanless 1973, Hereford 1977, Stewart and Suczek 1977, Middleton 1989, Middleton and Elliott 1990). Specifically, McKee, in the earliest definitive work describing the environment of deposition of the Tapeats Sandstone, interpreted the Tapeats Formation as representing deposition in a shallow (less than 20 m), subtidal to intertidal environment reflecting transgressive and regressive sequences (McKee and Resser 1945). This view was reinterpreted by Wanless (1973) who, on the basis of petrologic data from the overlying Muav Limestone, concluded that deposition of the Cambrian sediments occurred on a very shallow tidal to subaerial platform. Working in central Arizona, Hereford (1977) concluded the Tapeats was deposited as intertidal sand bars, beach, tidal flat and tidal channel sediments based on a variety of sedimentological features. Hereford's interpretation of the Tapeats Sandstone has been extended to the Tapeats sediments in the Grand Canyon area (Middleton 1989, Middleton and Elliott 1990).

Paleogeography of Cambrian and Pre-Cambrian Erosional Surface

At the onset of Paleozoic deposition, the pre-Cambrian paleogeographic surface exhibited low relief broken by a series of isolated monadnocks and by occasional granitic hills. These resistant cliffs of Shinumo Quartzite, some rising 250 m above the associated pre-Cambrian landscape, occur as a linear strike ridge trending to the northwest (Sharp 1940a).

Associated with the pre-Cambrian Shinumo Cliffs exposed in the Grand Canyon are Cambrian breccias or debris flows, first identified by Sharp (1940b) at Ninety-one Mile Canyon as a subaqueous "slide". The debris flow, containing large quartzite clasts from the Shinumo Cliffs, was deposited on the cliff-face and along the pre-Cambrian topographic relief, extending up to a kilometer or more from the monadnock.

The Shinumo Cliff and the associated breccias provide an opportunity to investigate the influence of the pre-Cambrian surface relief on Cambrian sedimentary processes and to re-examine the concept of an encroaching marine shoreline. Aspects of the breccias will be used to identify the conditions present during the deposition of the Tapeats Sandstone in the vicinity of the pre-Cambrian monadnocks.

Methods

Paleoslope measurements and sedimentological features were recorded from all outcrops in the Grand Canyon exhibiting significant pre-Cambrian topographic relief. These outcrops and the number of data collection localities include Red (4, collection localities), Mineral (1), Asbestos (4), Vishnu (4), unnamed canyon west of Vishnu [referred to in this paper as "Friday" Canyon] (2), Clear Creek (3), Zoroaster (3), Bright Angel (6), Phantom (3), Ninety-one Mile (6), Trinity (2), Dragon (2), Crystal (2), Shinumo (1), Galloway (2), Stone (1), and Tapeats Canyons (5), as well as the outcrop along the Kaibab Trail (1), the region above Phantom Ranch in the Tapeats Embayment (7), and Monadnock (3) and Hotauta (3) Amphitheaters (Fig. 1).

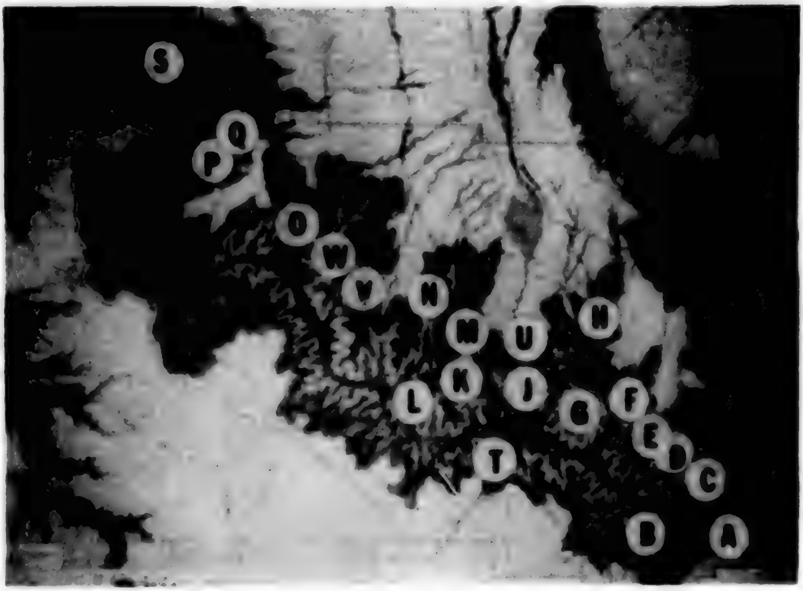

Fig. 1. Grand Canyon map: Outcrop and data collection localities: (A) Red Canyon, (B) Mineral Canyon, (C) Asbestos Canyon, (D) Vishnu Canyon, (E) "Friday" Canyon, (F) Clear Creek, (G) Zoroaster Canyon, (H) Bright Angel Canyon, (J) Phantom Creek, (K) Ninety-one Mile Canyon, (L) Trinity Creek, (M) Dragon Creek, (N) Crystal Canyon, (O) Shinumo Creek, (P) Galloway Canyon, (Q) Stone Canyon, (S) Tapeats Canyons, (T) Kaibab Trail, (U) Tapeats Embayment, (V) Monadnock Amphitheater, and (W) Hotauta Amphitheater (Huntoon et al. 1986).

Paleoslope measurements were generally made using a portable transit and rod, and occasionally using a Brunton compass when conditions prohibited use of the transit (Table 1). The paleotopographic detail required in a crucial region of Ninety-one Mile Canyon necessitated plane table mapping.

Table 1. Observable relief for Breccias and Tapeats Sandstone.

Location	Deposit	Relief (meters)
Red Canyon	Breccia: East wall	95 to >120
	Breccia: West wall	43
	Tapeats	20
Mineral Canyon	Tapeats	40.5
Asbestos Canyon	Tapeats	20
Vishnu Canyon	Breccia: East wall	91
"Friday" Canyon	Breccia: East wall	57
	Breccia: West wall	66
	Tapeats	71
Clear Creek Canyon	Breccia: West wall	>31
	Tapeats	57
Zoroaster Canyon	Tapeats	>16.4
Bright Angel Canyon	Breccia: East wall	33
	Breccia: West wall	77.6
Tapeats Embayment	Tapeats	61
Ninety-one Mile Canyon	Breccia: East wall	>92
	Breccia: West wall	167
	Tapeats	241
Crystal Canyon	Breccia: West wall	128.6
Monadnock Amphitheater	Breccia: East wall	113
East Fork	Breccia: West wall	160
West Fork	Breccia: East wall	87
	Breccia: West wall	73
Hotauta Amphitheater	Breccia: West wall	69
Shinumo Canyon	Breccia: East wall	>80
	Tapeats	>30
Galloway Canyon	Breccia: West wall	22
Stone Canyon	Breccia: West wall	30
Tapeats Canyon	Breccia	33

Seventy-four samples were collected from the Hakatai Shale, Vishnu Schist, Tapeats Sandstone and Bright Angel Shale along Ninety-one Mile Canyon (Fig. 2) for trace and major element analyses. X-ray diffraction data (summarized in Table 2) and X-ray fluorescence data (computed means and standard deviations summarized in Table 3) were compiled by a commercial testing laboratory.

Results

At 24 sites in Grand Canyon where Shinumo Quartzite paleocliffs are exposed, locally derived subaqueous debris flow breccias were identified. These sites range from Red Canyon at the eastern end of Grand Canyon to Tapeats Canyon in the west. Displaying complex sedimentological relationships with the overlying and underlying deposits, the breccias locally blanket pre-Cambrian topography including the cliff faces, as can be seen in localities where this relationship has not been destroyed by modern erosion. In those areas where the exhumed Shinumo Cliffs extend above the Tapeats and into the Bright Angel deposits, the breccias continuously underlie portions of both Tapeats Sandstone and Bright Angel Shale along the pre-Cambrian slope. For example, in Monadnock Amphitheater the original pre-Cambrian slope has been exhumed (Fig. 3). The breccia blankets this pre-Cambrian slope in unbroken continuity beneath both the Bright Angel Shale and Tapeats Sandstone over a vertical distance in excess of 150 m (Table 1). Similar relationships can be seen in outcrops at Red, "Friday", Clear Creek, Zoroaster, Bright Angel, Ninety-one Mile, Crystal, Shinumo, Hotauta, Galloway/Stone, and Tapeats Canyons. Breccias extend for vertical distances of up to 160 m and horizontally up to 2 km from the Shinumo outcrops. We walked these breccia outcrops in all possible localities and found a general absence of evidence for post-depositional erosion or reworking during the interval between deposition and final burial, as evidenced by the continuity of the breccia units and the absence of reworked breccia material in the immediately overlying Tapeats beds.

Clasts in the breccia flow range from pebble size to 10 m and larger. One large clast in Red Canyon contains a mine shaft driven by an ill-fated mining operation. Larger clasts 30 m or more in length were found occasionally in close proximity to the Shinumo Cliffs.

In many areas of the Canyon the basal Tapeats consist of alternating light and dark layers of well-sorted, medium to coarse grained, graded sandstone beds. The debris flows generally lie immediately above or within these lower Tapeats beds. Within the debris flows, the Tapeats sands form much of the matrix. In the west wall of Ninety-one Mile Canyon, portions of this basal Tapeats occur as rip-ups in the breccia (Fig. 4). In some areas near the cliffs, isolated Shinumo clasts are incorporated into the Tapeats Sandstone at various horizons (Fig. 5). In a number of localities paleoslope was determined

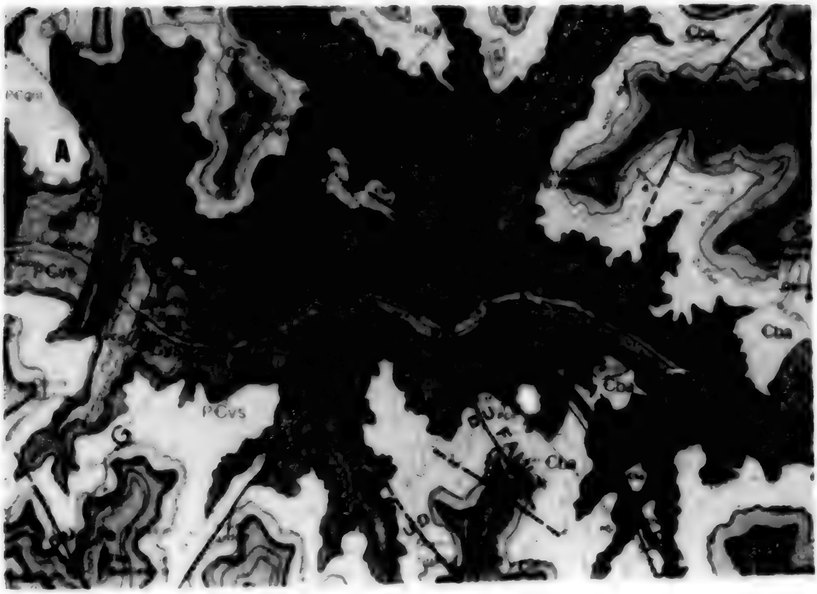

Fig. 2. Grand Canyon map showing the plateau (A) above canyon formed by Ninety-one Mile Creek to the right (Huntoon et al. 1986).

Table 2. XRD results.

Sample name	Major mineral	Minor minerals	Trace minerals
Tapeats Sandstone	quartz	mica, feldspar, hematite, kaolinite, calcite	
Hakatai Shale	quartz	feldspar, mica, hematite	kaolinite
Bright Angel Shale	quartz	feldspar, mica, kaolinite	calcite

Table 3. XRF results.

Formation	Number of samples	Mean Th/U ratio	Standard deviation
Tapeats Sandstone	47	2.6	0.17
Bright Angel Shale	5	2.6	0.06
Hakatai Shale	3	2.2	0.07

Fig. 3. Breccia (A) blanketing pre-Cambrian Shinumo Quartzite (B) and Hakatai Shale (C) and underlying Cambrian Bright Angel Shale (D) and Tapeats Sandstone (E) at Monadnock Amphitheater. (Breccia overlying Shinumo Cliff is <1 m thick.)

Fig. 4. Rip-up of Tapeats Sandstone (A) within the breccia near the base of the Tapeats Sandstone at Three Points near Ninety-one Mile Canyon. (Arrow indicates man pointing to base of rip-up for scale.)

for individual beds of Tapeats Sandstone (Table 1). The vertical relief over which single beds were deposited exceeded 50 m. In Ninety-one Mile Canyon where the highest Shinumo Cliff is preserved, infillings of Tapeats Sandstone were found in relict drainages atop the cliff, 250 m higher than the base of the Tapeats deposits adjacent to the cliff.

Sedimentary features observed in the Tapeats Sandstones located in the Tapeats Embayment include festoon cross-stratification and isolated herringbone cross-stratification occurring only in association with the monadnock, graded beds, planar cross-beds, and isolated Shinumo clasts within the sandstone.

XRD analyses revealed similar mineralogy for the Hakatai Shale, Tapeats Sandstone, and Bright Angel Shale (Table 2) with quartz dominating all of the units and glauconite visible in Tapeats Sandstone and Bright Angel Shale hand samples. Trace to minor presence of hematite, indicative of diagenetic alteration of the deposits, had little impact on the Th/U ratios. Mean Th/U ratios for the samples from Ninety-one Mile Canyon are 2.6 (Table 3). Based on a comparison of the means, these ratios for the Tapeats Sandstone and Hakatai Shale occurring in the breccia as matrix and the Bright Angel Shale do not differ appreciably.

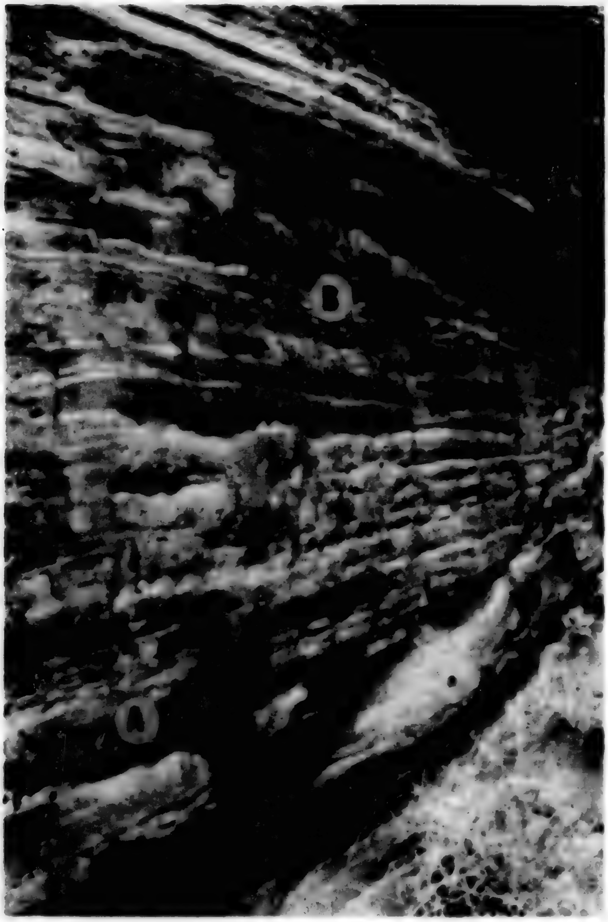

Fig. 5. Clasts outlined at (A) and (B) within bedded Tapeats Sandstone along the south Kaibab Trail. (Clasts are approximately 22 cm across.)

Discussion

Brecciated debris flows containing large clasts require high energy, fluidized depositional processes (Cook et al. 1972). Large clast sizes, synchronous deposition and ubiquitous occurrence of the breccias associated with the Shinumo Quartzite cliffs require a high energy source during Lower Cambrian deposition. The inclusion of large, matrix-supported clasts in the

Tapeats Sandstone suggests that this formation also was deposited under high energy conditions (Fig. 5). It seems likely that deposition of all of these units took place within a high energy marine system associated with the Shinumo Cliffs.

The alternating layers of light and dark sandstone commonly seen in the basal portion of the Tapeats Sandstone were documented previously by Sharp (1940a) and McKee and Resser (1945). Subsequently these beds, consisting of well-sorted, normal graded sands were identified as turbidites (Burgert 1972). This interpretation is consistent with a high energy, marine environment but inconsistent with deposition in a tidal marine environment.

Beds of Tapeats Sandstone blanketing the Shinumo paleocliffs typically show original dip parallel with the pre-Cambrian highs (McKee and Resser 1945). Similar relationships between sandstones and relict cliffs in the Ozarks were noted by Dake and Bridge (1932). In addition, the complex sedimentary structures in the Tapeats Sandstone against the Shinumo paleocliffs at the Tapeats Embayment suggests upslope flow of the sands during deposition. Muck and Underwood (1990) have documented such upslope flow in turbidity currents and have reproduced this effect in laboratory experiments.

In the 24 localities where debris flows, associated with the cliff face and occasionally in direct contact with the face, can be traced laterally into the basin, vertical distances exceed depths typically attributed to nearshore marine environments. Numerous beds of Tapeats Sandstone in the Grand Canyon display vertical relief of 50 m or more (Table 1). At Monadnock Amphitheater and other localities where exhumation of the Shinumo Cliff is occurring and the relationship between the breccia and the original cliff face is preserved, the lack of post-depositional erosion or reworking of the breccia precludes a Cambrian shore line in this region. In most of these localities, portions of the breccia were unprotected during the entire deposition of Tapeats Sandstone and during deposition of a significant part of the overlying Bright Angel Shale. The breccia was not covered entirely until Bright Angel Shale buried the associated Shinumo Cliff. The unreworked and widespread preservation of the breccia would require that it not only be covered by water, but that the unit exist below storm wave base. For this to be true, water depths in excess of 200 m would be required during the deposition of the Lower and Middle Cambrian sediments associated with the breccias and monadnocks in the Grand Canyon region.

In "Friday," Vishnu, Stone, Gallaway and Shinumo Canyons, and other localities where the relationship can be seen, Tapeats Sandstone is deposited directly against the Shinumo Cliff face with little evidence of erosion along the face that would be expected if the cliffs were subaerially exposed or formed part of a shore facies for extended periods of time (Fig. 6). This reinforces the previous conclusion that the cliffs were covered with water while the Tapeats sand accumulated, and thus, were protected from shoreline erosion. Again, water depths in excess of 200 m would be required.

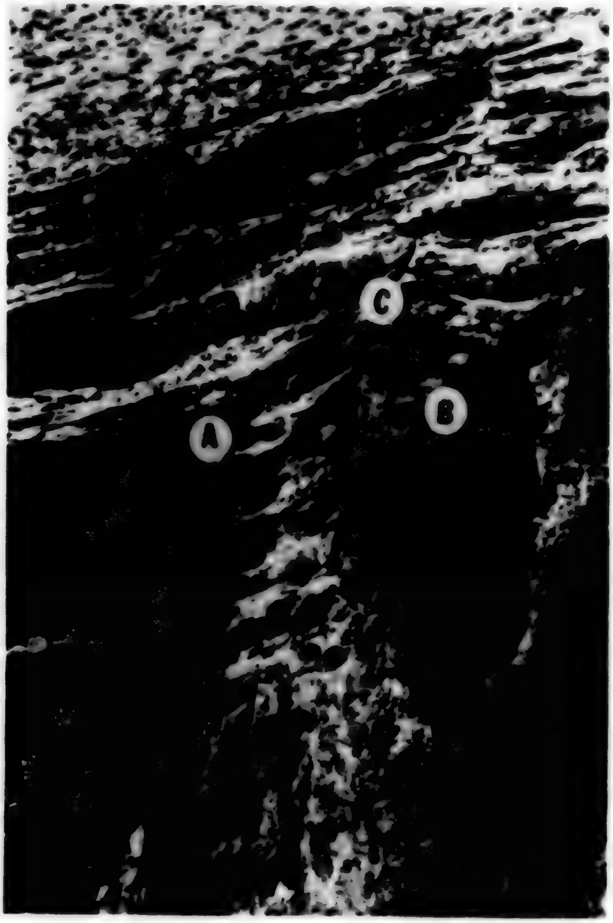

Fig. 6. Near the head of the west arm of Vishnu Temple, Tapeats Sandstone (A) abuts Shinumo Quartzite Cliff (B) with contact marked by line (C). (Tapeats beds are <1 m thick.)

Thorium/uranium ratios have been used to differentiate between oxidizing and reducing environments (Bhatia and Taylor 1981). Oxidation of uranium produces ratios in excess of 5.0 with reducing/low oxygen environments having Th/U ratio values less than 5.0. Samples from the breccia matrix in this research have a mean Th/U ratio of 2.6 (SD = 0.2) indicating a reducing environment consistent with deep water and low oxygen conditions (Table 3). Bhatia and Taylor (1981) also noted that reworking of the sediments would tend to increase the Th/U ratios to values greater than

5.0. This provides additional support for the interpretation that the breccias blanketing the pre-Cambrian surfaces associated with the monadnocks are undisturbed.

The presence of Tapeats Sandstone in relict drainages in the top of the Shinumo Cliff at Ninety-one Mile Canyon, 250 m above the surrounding Tapeats depositional surface, along with paleocurrent trends in the Tapeats Sandstones from northeast to southwest across the pre-Cambrian highs, requires water depths in excess of 250 m above the surrounding pre-Cambrian floor. In this research the presence of herringbone and festoon/trough cross-bedding in association with the upper reaches of the monadnocks indicates complex current activity concentrated near the tops of the pre-Cambrian cliffs. The lack of these features lower in the Tapeats Sandstone sections adjacent to the Shinumo paleocliffs suggests that such activity may be due to the effects of storm wave base near the apex of the monadnocks. If true, this would place the surrounding planar pre-Cambrian surface at depths greater than 250 m plus storm wave base. The primary objection that could be raised to this interpretation is based on the sedimentary structures and facies relationships attributed in the literature to shallow, nearshore marine environments (McKee and Resser 1945, Wanless 1973, Hereford 1977, Middleton and Elliott 1990). Caution is warranted in this application of paleoenvironmental interpretations due to the paucity of information available in regard to sedimentary structures and facies relationships in modern deep water environments. A wide variety of large scale features have been described (Sharp 1940b, McKee and Resser 1945, Middleton and Elliott 1990) in the Grand Canyon; however, the application of sedimentary structures to shallow water models may also apply to the as yet poorly understood deep water settings.

Conclusions

During deposition of the Tapeats Sandstone in the Grand Canyon, water depths exceeded 200 m plus the depth to storm wave base. This conclusion is suggested by the following data: (1) submarine breccia flows blanket the pre-Cambrian surface with over 150 m of vertical relief; (2) flows appear undisturbed by any event subsequent to subaqueous emplacement; (3) apparent absence of Cambrian erosion of the pre-Cambrian cliff faces precludes extended exposure as a shallow, high energy system; (4) Th/U ratios are characteristic of unreworked, deep-water deposits; and (5) the occurrence of Tapeats Sandstone atop the highest Shinumo Cliffs requires water depths over a vertical relief in excess of 200 m for the surrounding pre-Cambrian surface. Based on the data in this study, the authors are reluctant to discount the deep-water model solely on facies relationships easily found in modern shallow water settings but difficult to document in deep water deposits.

Acknowledgments

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Cultural Resources

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Preliminary Results of Noise Monitoring in 1995 in Bryce Canyon National Park

Dan A. Foster[1]
Richard M. Bryant

National Park Service
Bryce Canyon National Park
Bryce Canyon, Utah 84717

Abstract: Staff at Bryce Canyon National Park conducted noise monitoring surveys from 30 May to 31 August 1995 at five sites using the 15-second Leq method. Noise levels from helicopters, planes, jets, and other mechanical means, as well as natural or background noise were monitored. Aircraft were heard park-wide an average 18.8% of the time with an average of 36.4 decibels. Site-specific information is presented on peak decibel levels, average noise levels, and number of aircraft overflights.

Key words: Aircraft, monitoring, noise, overflight.

Visitation to Bryce Canyon National Park by the general public continues to increase on a yearly basis. Impacts from visitation are coming in a variety of ways, but park management has become increasingly aware that noise from mechanical sources, particularly aircraft, has the potential to undermine the natural quiet for which the park has been noted.

Use of aircraft to travel to, and view Bryce Canyon National Park has been possible almost from the park's inception. Even before the park was created in the early 1920s, a U.S. Forest Service plan for development included location of a suitable site for "Aeroplane landing" (Scrattish 1985). By the mid-1930s the development of an airport just two miles north of the park was underway. An emergency landing strip with a hangar was completed by 1937 under the combined efforts of the Work Projects Administration, Civilian Conservation Corps, and Garfield County (G. Pollock, Bryce Canyon Airport, personal communication).

In 1977, a private corporation, based immediately north of the park, began offering helicopter and fixed wing tours of the park and region (P. Cox, Bryce Canyon, Utah, personal communication).

In 1995, park staff began a program to monitor noise levels throughout the park. Purposes of the study were to aid in the establishment of baseline data on natural quiet and noise source types within the park, the percent of time these are heard, and the noise equivalent levels (Leq) in decibels.

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[1] Present address: Nez Perce National Historical Park, Spalding, Idaho 83540.

Methods

The project was coordinated by the Division of Resource Management aff at Bryce Canyon National Park. Surveyors were volunteers and park aff.

Five sites were established for monitoring noise from low to high levation and included canyon rim and back country locations (Fig. 1). The sites were adjacent to the escarpment of the Paunsaugunt Plateau, which consists of a series of geologic formations eroded into vertical structures known in geologic terms as "hoodoos." This is also the major feature of interest for park visitors, as it dominates the area and provides vistas of exceptional quality to the surrounding areas. The Fairyland site (UTM: 400173E, 4165835N), was adjacent to the Fairyland Loop Trail, underneath the escarpment or rim, on a ridge sparsely vegetated with ponderosa pine (*Pinus ponderosa*) and a scattered assortment of manzanita (*Arctostaphylos patula*) and grasses, at an elevation of 7,480 feet. The Water Tanks site (UTM: 396731E, 4163898N), was adjacent to the Rim Trail mid-way between the Sunset Point and Inspiration Point overlooks, on the top of the rim, with a heavy vegetative cover of ponderosa and manzanita, at 8120 feet elevation. The Swamp Canyon site (UTM: 393172E, 4159728N), was adjacent to the Swamp Canyon and Sheep Creek trails, beneath the rim, with a heavy vegetative cover of ponderosa, manzanita, and Gambel oak (*Quercus gambelii*), at an elevation of 7,720 feet. The site in Agua Canyon (UTM: 389033E, 4152198N), on the Agua Canyon Connecting Trail switchbacks below the rim, was at an elevation of 8,560 feet, in an amphitheater with a sparse vegetative cover of bristlecone pine (*Pinus longaeva*). The last site, Bristlecone (UTM: 390761E, 4147658N), was on the Bristlecone Loop Trail, at 9,040 feet elevation, surrounded by bristlecone pine, Engelmann spruce (*Picea engelmannii*), white fir (*Abies concolor*), and Douglas fir (*Pseudotsuga menziesii*).

Equipment and training were obtained from the Washington Office of the National Park Service. Equipment protocols, monitoring procedures, and spreadsheet analysis were derived from "Selecting a Simplified Method for Acoustic Sampling of Aircraft and Background Sound Levels in National Parks" (Miller et al. 1995). The equipment used was a tripod-mounted CEL 269 Sound Level Meter with wind screen and CEL 282 calibrator. The monitor provided measurement of sound levels from 30 to 100 decibels. This equipment is easy to use because there are few steps for setup and operation. Before and after calibrations provided efficient means to ensure proper equipment function. A digital readout wind meter was also used to determine wind speed.

The procedure used has been described as the 15-second Leq method. A log sheet was used to annotate the noise "equivalent" level (Leq) in decibels for every 15 seconds over a 1 hour time period. The Leq was coded as the

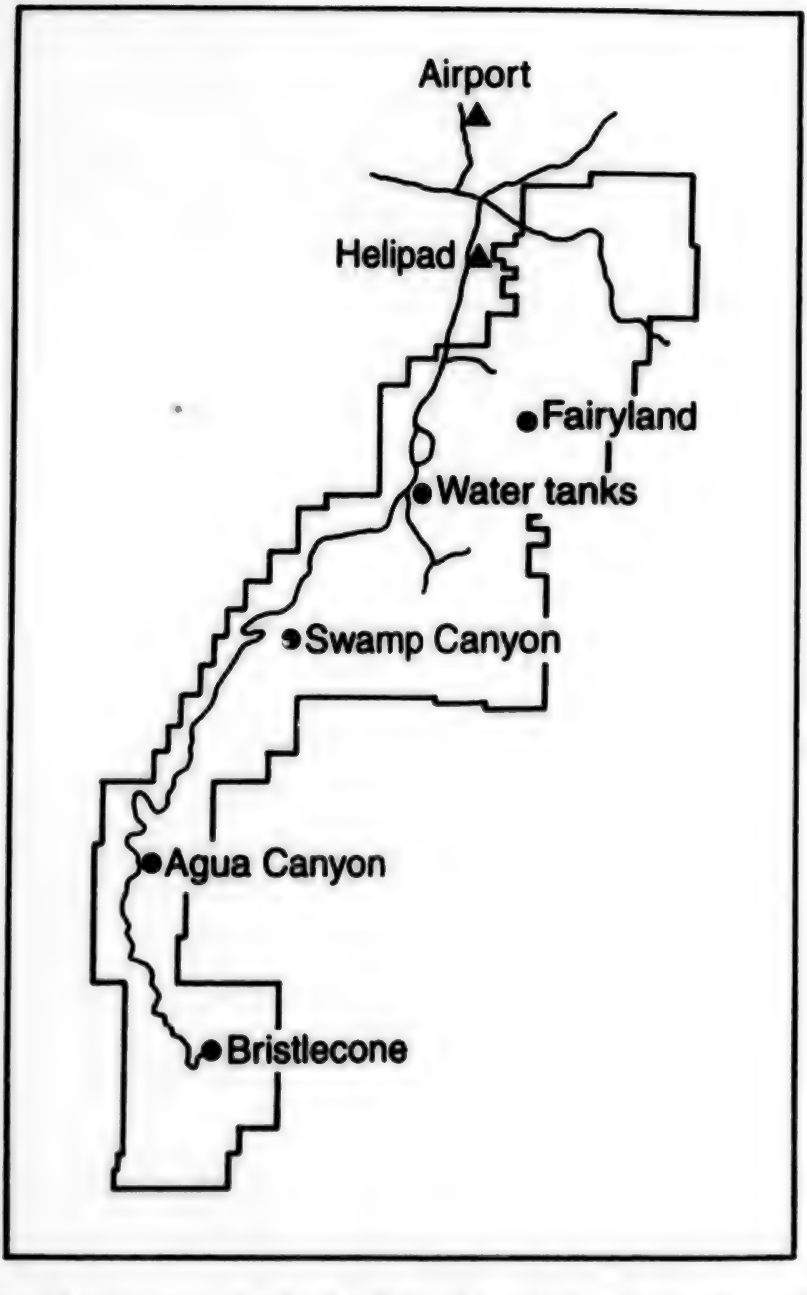

Fig. 1. Bryce Canyon National Park boundary, noise monitoring sites, and aircraft landing locations.

sound source the observer heard at the end of each 15-second time period. The sound source was determined by a hierarchy. If an aircraft was heard, it was recorded on the data sheet at the level indicated on the monitor. If no aircraft was heard, but other human sounds were audible, then an "other-human" annotation was made. If no mechanical noise was heard, then natural sound was noted at the appropriate level.

Four sites were monitored for 13 hours, while one site, Agua Canyon, was monitored for 12 hours due to lack of personnel time. We varied the monitoring hours and days of the week, to sample across daylight hours and days. No monitoring was undertaken if winds of 10 miles per hour or greater were experienced.

Each Leq column on the data sheets was tabulated and the results entered into spreadsheet software provided by the Washington Office of the National Park Service. The software converted the totals of each column into aircraft noise doses. This eliminated the need for training of park staff in these computations and ensured consistency in the accomplishment of complex mathematical calculations. From the spreadsheet calculations the following information was obtained, for each site by hour: (1) percent of time aircraft was audible; and (2) Leq for aircraft noise.

Results

After 64 hours of monitoring at the five selected sites we found, park-wide, aircraft could be heard an average of 18.8% of the time with a standard deviation of 7.3. Table 1 presents the percent of time aircraft are heard at each site with accompanying standard deviations. To arrive at these numbers we simply averaged the hourly readings for each site. For the purposes of this study, we defined helicopters as any rotary aircraft. Planes were fixed-wing, low altitude aircraft. Jets were high altitude aircraft. A graph representation of the same information is presented in Fig. 2, with the sites listed in a north to south orientation from left to right.

Because of limited staff, we were not able to take enough readings scattered through the daylight hours to determine the number of overflights by hour. However, we did separate the data into general blocks of time representing morning (6:00 a.m. to 11:00 a.m.), midday (11:00 a.m. to 4:00 p.m.), and evening (4:00 p.m. to 9:00 p.m.). Data in these time frames indicated that helicopter and plane overflights gradually decreased from morning until evening (helicopters - 1.5/hour in the morning, 1.1/hour in the midday, 0.7/hour in the evening; planes 1.3/hour in the morning, 1.1/hour in the midday, 0.3/hour in the evening), while jet traffic remained relatively constant throughout the day (4.9 in the morning, 4.1 in the midday, 5.8 in the evening).

Table 1. Percent of time aircraft heard at monitoring sites. Numbers in parentheses are the standard deviations for the decibel levels.

	Fairyland	Water Tanks	Swamp Canyon	Agua Canyon	Bristlecone
Combined aircraft	29.2	19.3	21.8	12.4	11.4
	(18.8)	(15.3)	(9.9)	(7.2)	(6.5)
Jet	13.1	11.9	13.4	8.6	9.9
	(14.2)	(8.6)	(8.0)	(5.6)	(5.6)
Helicopter	11.5	3.5	5.5	2.7	1.0
	(11.9)	(4.7)	(7.1)	(5.8)	(3.5)
Plane	4.2	3.8	3.1	1.2	0.6
	(3.4)	(3.7)	(3.3)	(1.5)	(2.1)

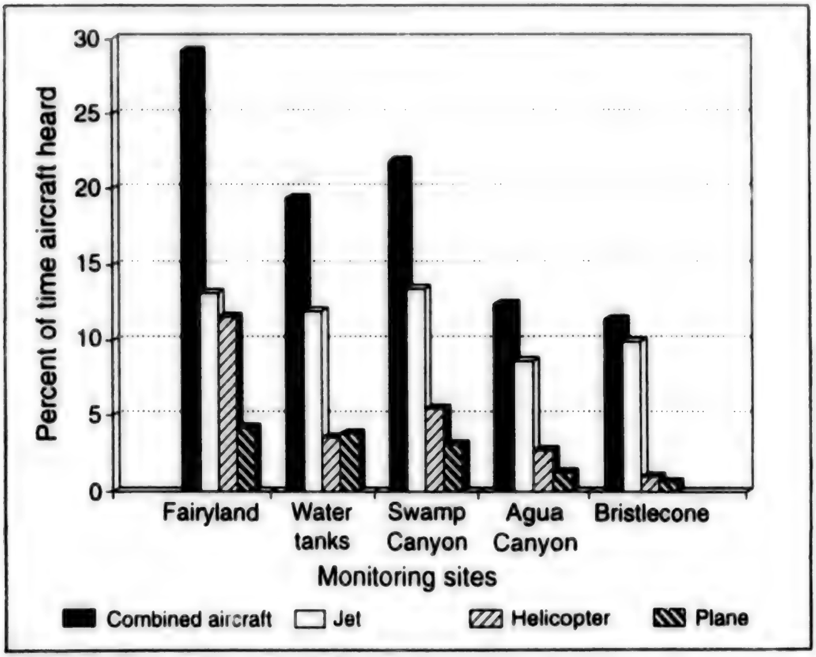

Fig. 2. Percent of time aircraft heard at monitoring sites.

Peak decibel levels recorded from the meter at each site by aircraft type were Fairyland (jets - 58, planes - 59, helicopters - 70); Water Tanks (jets - 58, planes - 56, helicopters - 53); Swamp Canyon (jets - 56, planes - 57, helicopters - 62); Aqua Canyon (jets - 61, planes - 54, helicopters - 70); and Bristlecone (jets - 58, planes - 56, helicopters - 51).

Discussion

In a north-south orientation of the sites, it was evident that the sites in the north experience greater amounts of noise from aircraft overflight. These sites were not only closer to the airport and helicopter pad, but were lower in elevation and also lie closer to flight patterns for optimal viewing of the main amphitheater and geologic formations of the park.

One phenomenon we noticed was the level of noise experienced by the observer changed with respect to the position of the aircraft engines or rotor. For example, high altitude jets were rarely heard until directly overhead, but were heard for long time periods after passing. The same is true for planes, with the exception that they were more easily perceived on approach to the observer, because of lower flight altitudes. Helicopters, on the other hand, were heard for tremendous approach and retreating distances, depending on the position of the observer with respect to the helicopter rotors. For example, the peak decibel level recorded for helicopters (70 decibels) was at both Fairyland and Agua Canyon. These sites were both below the normal flight altitude of all aircraft. Fairyland is within close proximity to helicopter tour operation flight patterns. In comparison, the Bristlecone and Water Tanks sites, both located above the rim at elevations above or horizontal to normal helicopter flight altitudes had peak readings of 51 and 53 decibels, with only Water Tanks being in close proximity to normal tour operations. If the observer was below the level of the rotor, the noise levels were much higher than if horizontal to or above. Gradual decreases in overflights of helicopters and planes from morning to evening may result from geographic orientation of the park. With the escarpment exposed to the east, greater viewing may be obtained earlier in the day from the air.

There are many factors affecting the sound levels from aircraft. Some of these include: (1) aircraft height; (2) slant distance of the aircraft to the observer; (3) atmospheric absorption and aircraft source spectra; (4) attenuation due to intervening hills and heavily wooded areas; (5) attenuation of ground or ground cover that softens noise levels such as grassland; and (6) how the sound of the aircraft is defined, such as total sound exposure, duration, or the maximum sound (Anderson and Horonjeff 1992).

Because the equipment used for this study would not measure noise below 30 decibels we were constrained to research other studies to detect ambient or background noise levels. During the late 1970s, monitoring of noise levels within the park was conducted in conjunction with a proposed open pit coal mine near the park. During the day, in absence of strong winds, ambient sound levels frequently fell below 20 decibels. This is comparable to sound levels experienced in high quality recording studios (Foch and Oliver 1980).

The vast majority of helicopter overflights in the park are from the private tour operator located just outside the park to the north. This service provides visitors a unique view of the park and the geology not obtainable from the ground. Of the complaints received at the park, the most common are consistently concerned with helicopter noise and overflight. These complaints generally come from visitors who have made an effort to seek the solitude and quiet of back country areas. Although this study shows that helicopter overflights create a deterioration of natural quiet for the time they are heard, a significant amount of the aircraft noise heard is generated by jet and plane traffic. Jet and plane traffic may be "tuned out" by the general public and accepted as part of the normal spectrum of noise, as few complaints concerning these are received. It is also of interest to note that the areas where the solitude experiences are probably best experienced are the areas where the helicopter overflight percentages and noise levels are the least.

The fixed-wing overflights are from two primary sources. The first source is scenic and sightseeing flights bringing visitors to the airport. These include single- and twin-engine aircraft with a capacity of a few to about 20 passengers. The second group is private aircraft flying to the area. In the fall of 1995, the Federal Aviation Administration changed the Bryce Canyon Airport designation from general aviation to commercial due to increased use of the airport facilities. As of mid-November 1995, it was estimated that 1,200 aircraft had landed at the airport during the year. Use of the airport is projected to increase at an annual rate of 12 to 15%, from both scenic tours and private aircraft, based on recent trends (G. Pollock, Bryce Canyon Airport, personal communication). Although there have been, and are now, many users for the airstrip at Bryce Canyon, the original designation was for an emergency landing strip for commercial aircraft. The park and surrounding area lie under some of the busiest commercial air traffic flyways in the country. These include, but are not limited to: (1) Las Vegas, Nevada to Denver, Colorado; (2) Salt Lake City, Utah to Phoenix, Arizona; (3) San Francisco, California to Denver, Colorado; and (4) Los Angeles, California to Denver, Colorado. This understanding provides a more complete picture as to the levels of noise experienced in the park by commercial jets.

This research provides a better understanding of the types of noise occurring in the park, including the amount of time non-natural noise occurs. It will help establish baseline data to aid park managers in working to mitigate the degradation of "natural quiet" within the park and surrounding area. The potential increase in aircraft traffic may have serious impacts to this valuable natural resource.

Acknowledgments

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Prehistoric Agriculture at High Altitude on the Northern Colorado Plateau

William B. Fawcett
Jason R. Bright

Sociology, Social Work and Anthropology
Utah State University
Logan, Utah 84322-0730

Abstract. Archaeological investigations east of Moab, Utah have revealed an ancient agricultural field with linear water control features at a high elevation (7,500 feet). Excavation in a nearby cave, believed to be associated with the use of this agricultural field, recovered many diverse cultigens in fine stratigraphic contexts. We believe these deposits date from the last half of the first millennium A.D. Human occupations of the cave were consistently brief and ephemeral. Human subsistence varied between the extremes of full reliance on wild species and heavy use of domesticated cultigens.

Key words: American southwest, Anasazi, egalitarian, Fremont, horticulture, hunter-gatherers, mobility, Pueblo.

In the summers of 1994 and 1995 Utah State University conducted two 10-day field sessions east of Moab, Utah, to excavate portions of a large dry cave and to investigate a possible agricultural field. Both sites are at higher elevations (7,500 feet) than similar archaeological sites elsewhere on the Colorado Plateau (Fawcett 1994:15, 17; Table 1). Unlike Coombs Cave and Field, all of the other agricultural fields and water control features in Utah are near former Puebloan villages. In this article, we summarize the 1994–1995 field work and present some preliminary findings concerning early agriculture under marginal conditions near the boundary between the Anasazi and Fremont.

An Agricultural Field With Water Control Features

Perhaps the most surprising part of our work is the discovery of an agricultural field. Coombs Field (42GR2685) is located far (5.6 km) from permanent water sources.

Table 1. Elevation of Puebloan agricultural fields and water control features in Utah.

Elevation (in feet)	Number of sites
<5,000	10
5,001–5,200	13
5,201–5,400	10
5,401–5,600	10
5,601–5,800	8
5,801–6,000	14
6,001–6,200	13
6,201–6,400	11
6,401–6,600	17
6,601–6,800	12
6,801–7,000	9
7,001–7,200	9
7,201–7,400	4
7,401–7,600	2

Source: Utah IMACS computer system, July 3, 1995.

A dense scatter of stone artifacts originally drew our attention to this site. Closer inspection revealed a series of nine rock alignments (Fig. 1:F2–10). They are composed of shaped sandstone slabs, including fragments of manos and metates. The incorporation of metates and manos into the alignments may be evidence for both the long-term use and maintenance of this field and the processing of crops in the vicinity of the field. Other rocks for construction of the alignments probably came from sandstone outcrops along nearby washes.

Woodbury (1961) refers to such linear stone alignments along contours as linear borders. Each alignment follows the contours across a pinyon and juniper-covered slope between two eastward-draining washes. They can be traced for no more than 40 m. At either end erosional gullies have cut through them to reveal sandstone slabs stacked several courses high. Between the gullies, the rock alignments are more poorly exposed. Linear arrangements of oak trees follow the projected course of the buried portions of the alignments. Together, the rocks and trees have trapped sediment behind them, so that the slope appears to be terraced. The field, as defined by the linear borders, covers about an acre (0.4 ha).

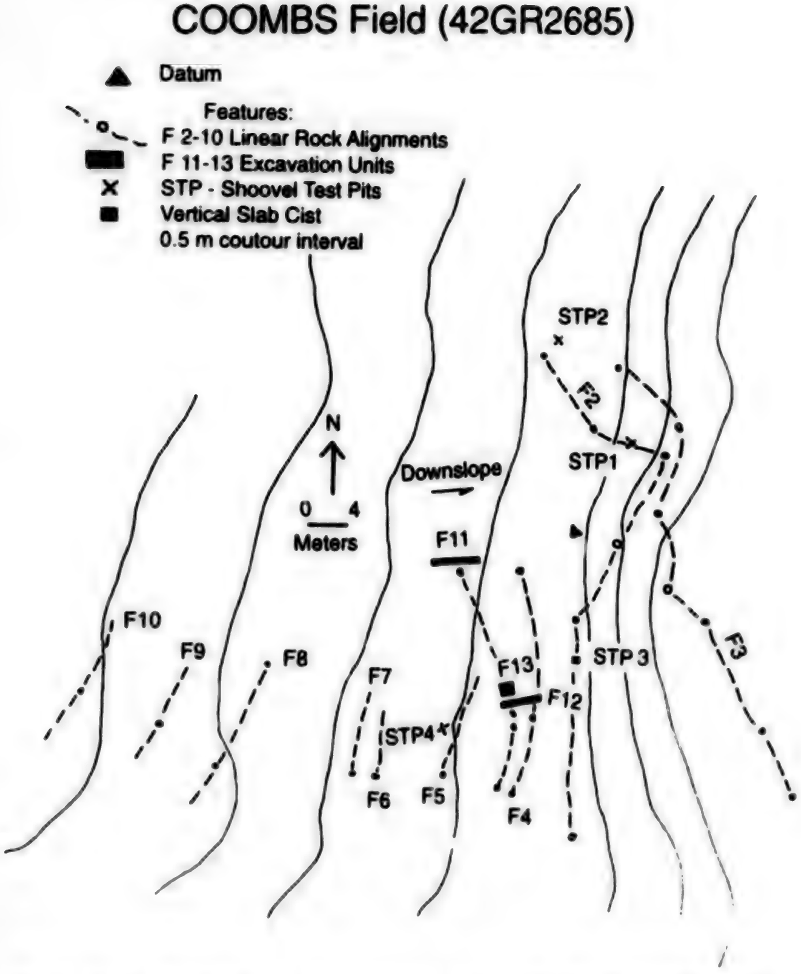


Fig. 1. Rock alignments and excavations in Coombs Field (42GR2685).

In 1994 we excavated shovel tests (STP 1–2 and 4) behind the alignments and in a cist (STP3) to collect soil samples for pollen analysis (Fig. 1). A side-notched arrow point, similar to others found in the cave, was found during the removal of the sample within the vertical-slab cist. These points do not fit neatly into existing types possibly because the sites are located near the Fremont-Anasazi boundary. Parts of what are believed to be a stalk of uncharred corn plant were also found near the datum.

In 1995 we excavated three trenches (F11–13) that crosscut the projected buried portions of the alignments (Fig. 1). Buried alignments of rocks were found in the predicated locations at a depth of about 0.5 m. Many of the buried rocks were broken. Some rocks appear to have been shaped. Pieces of manos and metates were included among the rocks. Some of the wood charcoal in the deposits around and above the rocks can be attributed to fires used to clear vegetation from the field.

The quantities of chipped-stone artifacts in the trenches were highest at and just above the buried rocks (Fawcett and Bright 1996). From the predominance (>90%) of interior/tertiary flakes we infer that most of the flakes were produced during tool finishing and resharpening. Some of the flakes appear to have been used as cutting and scraping implements, perhaps associated with agricultural activities. In light of the large numbers (n = 709) of flakes and scarcity of tools (n = 2) and cores (n = 4), much of the tool finishing and resharpening was probably to prepare tools for use and discard away from the field, and possibly for non-agricultural activities. Investigations at Coombs Cave provide further evidence that the prehistoric inhabitants continued to mix farming with hunting and gathering activities throughout the second half of the first millennium A.D.

The Cave

Coombs Cave (42GR383) overlooks a pinyon-juniper covered mesa dissected by several washes. Coombs Field is located on the mesa about 300 m to the southeast of Coombs Cave (Fig. 2). We infer that the occupants of the cave were also responsible for the field based on similarities in arrow points at both sites and the presence of various cultigens, which may have been grown in Coombs Field, in some stratigraphic layers within the cave.

Coombs Cave is of average size (375 m^2) among those on the Colorado Plateau, but it is one of the smallest and most distant from water among the caves with corn (Fawcett 1994:17). The diversity of cultigens--corns, beans, squash, gourds, and possibly sunflowers and cotton--in the deposits exceeds that at most other sites located at higher-elevations on the Plateau (cf., Matson 1991, Fawcett 1995).

By the time we visited the cave, vandals had dug a series of holes into the upper meter of deposits across the rear of the cave (Fig. 2). While searching for elaborate artifacts, such as textiles, hafted-tools and pots, they destroyed the stratigraphic context of the ecofacts and features over about 50% of the site, down to a depth of at least a meter. Most of their digging failed to penetrate the dense layer of rocks (including large boulders) created when large quantities of sandstone fell from the ceiling of the cave. We know from archaeological investigations of other intact caves (Matson 1991, Janetski 1993) that the inhabitants organized their activities to take into account differences in natural light, accessibility, dust, noise, slope, and micro-climate. The vandals' efforts have ensured that we will never be able to

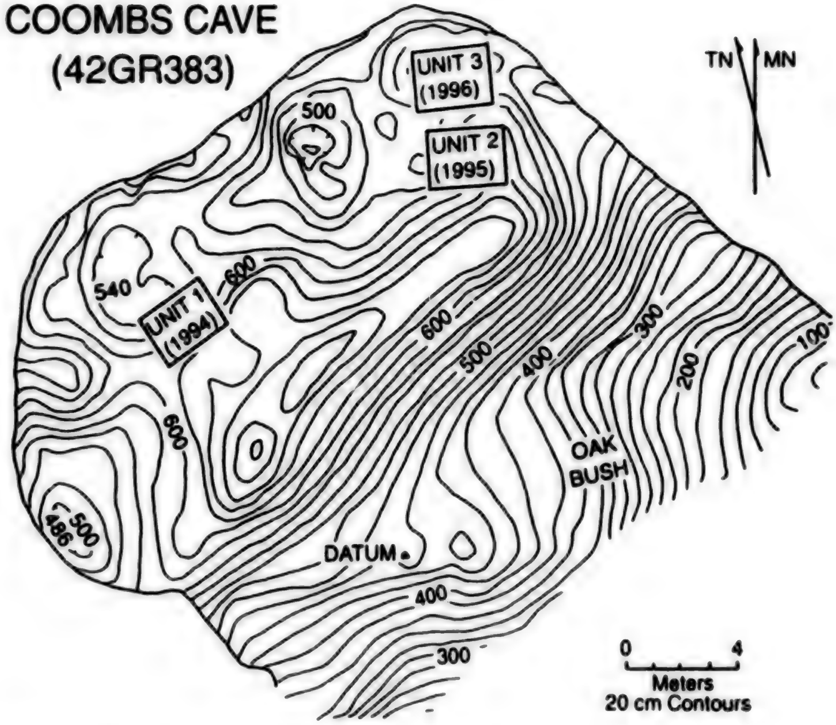
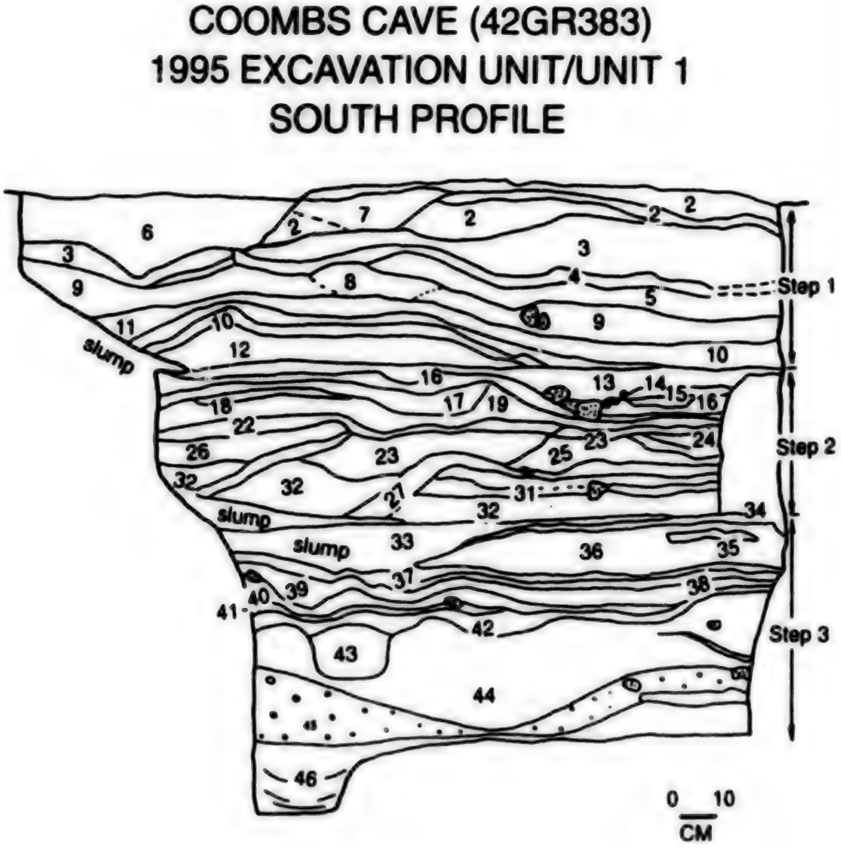


Fig. 2. Plan map of Coombs Cave (42GR383).

investigate questions concerning the spatial organization of Coombs Cave. Instead, our research examines changes over time in subsistence, climate, and regional land-use.

Three excavation units have been carefully excavated into the cave deposits (Figs. 2–4). This article concentrates on the 1994 and 1995 units because analyses of materials from the 1996 unit has barely begun. The units were located adjacent to the vandals' pits to take advantage of the exposed stratigraphy and avoid damaging more intact portions of the cave.

The deposits consist of extremely loose fine sand derived from the decomposition of the sandstone ceiling of the cave. Rocks rarely occur, except in cultural features (such as hearths) or in the roof-fall. Some large rocks, probably displaced from the roof-fall, occur in the vandalized deposits. Humans introduced grass, juniper bark, cactus, and other plants into the deposits, along with charcoal, artifacts, bones, and refuse. Layers of grass and plant fibers help to stabilize the sand and to provide clues for deciphering stratigraphic relationships.



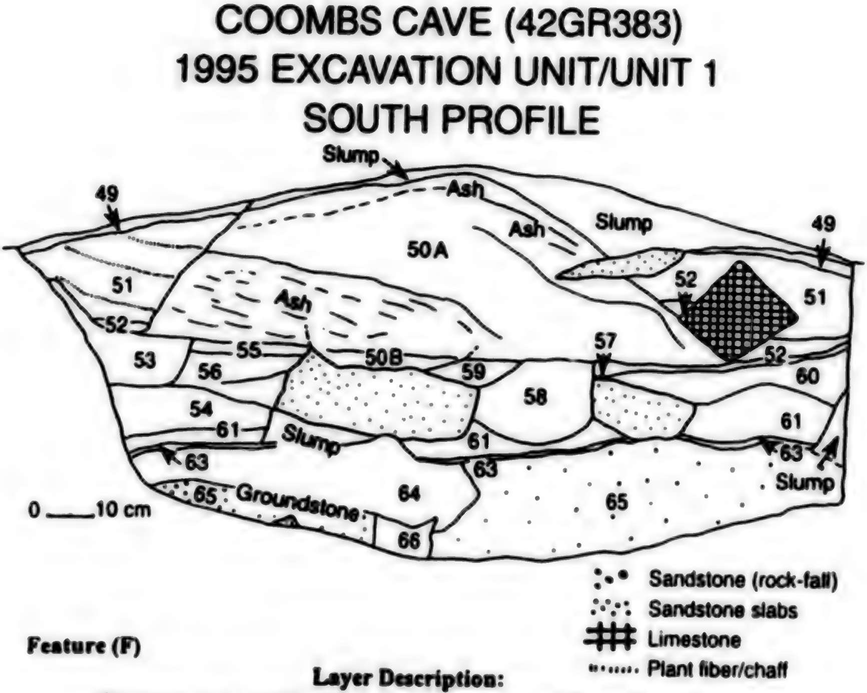
o.	Layer Description:
1	Very fine grey-brown loose sand (dust - F3)
2	Fine grey-brown sand with grass chaff & charcoal, relatively sterile (F5)
3	Sterile medium-texture brown sand with charcoal (F6)
4	Lighter brown sand (similar to F5) with sandstone rubble, charcoal & some grass chaff, relatively sterile (F7).
5	Charcoal-stained fine sand with some charcoal, small sandstone rocks, juniper, charred pine nuts & grass (F8-9)
6	Vandal pit with mixed deposits of charcoal, small sandstone & grass chaff (F2)
7	Shallow-basin shaped hearth with sandstone rocks & pine cones (F4)
8	Shallow-basin shaped hearth with sandstone rocks, pine nuts, yucca leaves, coprolites & cordage (F10)
9	Medium-texture brown sand with sandstone rocks, snails, corn, matted fiber, oak leaves & cordage (F12)
10	Light colored sand with coarse grass, sandstone, yucca fiber, juniper bark & charcoal (F13)
11	Dark charcoal stained sand with grass & pine parts (F11) associated with fire hearth (F10)

Fig. 3. Profile of the 1994 excavation (Unit 1) at Coombs Cave (42GR383).

12 Medium-dark charcoal-stained sand with small sandstone rocks, oak leaves, & grass chaff, flakes, pine parts & coprolites (F14)
13 Loose sandy disturbed deposits (bottom of first step/top of second - F15)
14 Dark organic-rich fine sand with charcoal (F16)
15 Shallow-basin shaped hearth with sandstone rocks, seeds, pine parts, grass, juniper bark & potsherds (F17) dug into layer below (F18)
16 Loose sand with numberous sandstone rocks (F18)
17 Grey-brown loose sand with corn, grass, flakes, bone & charcoal (F19)
18 Shallow-basin shaped hearth with charcoal, grass, bone, flakes, yucca leaves, pine & juniper parts & cacti remains (F20) dug into layer below (F22)
19 Dark brown sand with charcoal (F22) associated with hearths (F18 & 20)
20 Shallow-basin shaped hearth with charcoal, bone, cordage, grass & juniper bark (F21) dug into F22.
22 Fine grey-brown sand loose sand with sandstone rocks - relatively sterile (F23)
23 Loose light-colored fine sand with charcoal, sandstone rocks & chaff - relatively sterile (F24)
24 Shallow-basin shaped hearth with sandstone rocks, charcoal, grass, pine cones & bone (F25) excavated into layer below (F26)
25 Sand with fine chaff & charcoal, &corn cob, coprolite, bone & mano (F26)
26 Shallow-basin shaped hearth with sandstone, charcoal, mano, bone & flake (F27) dug into layer below (F28)
27 Medium-dark fine sand with charcoal & grass (F28)
28 Shallow-basin shaped hearth with charcoal, sandstone, grass chaff, flakes, corn & coprolite (F29)
29 Dark sand with grass, charcoal, corn cob, metate, sandstone & cordage (F30)
30 Medium-dark charcoal-stained sand with sandstone, bone & grass (F31)
31 Shallow-basin shaped hearth with charcoal, sandstone, bone, pine nuts & corn (F32)
32 Medium-dark sand with charcoal, sandstone, potsherds, bone, yucca & flakes (F33)
33 Sandy disturbed deposits (bottom of second step/top of third - F34)
34 Light sand with biface, grass & charcoal (F35)
35 Shallow-basin shaped hearth with sandstone & charcoal (F37) excavated into next layer (F38)
36 Loose medium-dark sand with charcoal, sandstone, grass, seeds, flakes & bones (F38)
37 Loose light-color sand with some sandstone, charcoal, grass, corn & flakes - relatively sterile (F39)
38 Dark sand, relatively sterile (F41)
39 Lighter sand, relatively sterile (F41)
40 Even lighter sand, relaively sterile (F41)
41 Very light-colored sterile sand (F41)
42 Mixed/disturbed sand
43 Deep Pit (not observed until profile was drawn)
44 Loose grey- brown sand with few flakes, yucca leaves, a potsherd, corn kernal & bone - relatively sterile (F43)
45 Light yellow to red-brown sandstone dust (F44) overlying dense layer of sandstone rocks (F45) - Roof-fall
46 Heavily-fired hearth in a pit with charcoal (F47)
47 Unexcavated, loose light brown sand - relatively sterile (F48)

Note: (F#) = Feature Number

Fig. 3. Concluded.



Feature (F)

Layer Description:

Compact grey sand with some grass, charcoal & small sandstone rocks

Large deep basin-shaped hearth surrounded by multiple lenses of ash & grass chaff from several cycles of hearth cleaning & reuse

Light tan/brown loose sand with abundant grass fiber

Dark brown sand with charcoal ash, possibly from cleaning out of F50

Loose mixed ash, charcoal & pine parts - possibly vandals backdirt

Light grey sand with some charcoal, sandsone & juniper bark

Sand with light scatter of grass chaff, stained at base

Thin charcoal & ash stain, cutting through F60

Light tan sand - mostly sterile

Basin hearth with as, charcoal & artifacts & evidence for multiple episodes of clean-out and reuse excavated into F57 and cutting through F

Ash & charcoal stains from cleaning of F58 - Bottom is fired & excavated into F57

Abundant grass fiber at base of loose light-grey sand

Dark grey sand with jumbled loose & coarse sandstone, charcoal & pine parts

Rodent burrow filled with charcoal & pine parts - mostly sterile

Thin layer of dark sand above roof-fall

Loose brown sand with charcoal, plant fiber & artifacts mixed in sandstone rocks (roof-fall)

Massive sandstone boulders with fine yellow sand (dust) from roof-fall. Fire blackening is present on some sandstone slabs

Plant fiber below(?) the roof-fall

Fig. 4. Profile of the 1995 excavation (Unit 2) at Coombs Cave (42GR383).

Excavation in such deposits is extremely difficult, because they are prone to slumpage. By stepping the unit inwards as the vertical face approached 0.5 m, we avoided major slumpage, but were also unable to expose much of the deeper deposits.

Stratigraphic levels were defined on the basis of content, texture, color, and compactness. Most levels were only a few centimeters thick (Figs. 3–4). They were assigned feature numbers and excavated in reverse order from their deposition. Artifacts and ecofacts exposed *in situ* were plotted on plans kept for each stratigraphic level. Except for the 1,000-cc special columns, the entire fill was dry-sieved through 0.125 inch mesh. The special columns were retained for pollen, soil, and macrobotantial analysis, especially of finer materials that would pass through the 0.125 inch mesh. In two years, we have removed about 3 cubic meters through well-documented scientific excavation. The vandals probably moved this much dirt in a few hours.

We took a very conservative approach in distinguishing between intact and disturbed (vandalized) deposits. Disturbed deposits appeared as loose sand with larger artifacts and ecofacts that were jumbled together with little evidence of size-sorting or consistent directional orientation. Larger rocks, probably from the roof-fall, occur more frequently in the disturbed deposits than in those believed to be intact. In contrast, intact deposits were more compact. Darker stained layers with charcoal, plant fiber and grass, other ecofacts and artifacts were separated by more sterile layers comprised of finely layered sand. Objects and particles exhibited consistent patterns of orientation, and did not appear to be jumbled and mixed. The vandals also introduced recent objects (e.g., filter masks, matches, cigarettes, gum wrappers, plastic) into the deposits. In some instances, vandalized deposits or backdirt can appear to be stratified in terms of color and particle size, but can still be distinguished by the relative absence of compactness and particle orientation present in intact deposits.

We initiated our excavations by carefully removing the disturbed deposits within a vandal pit to expose a vertical profile. We continued to peel back the profile, until we were certain that the deposits were intact. The unit was laid out and stratigraphic excavation begun down into the intact deposits. As each stratigraphic layer (or feature) was exposed we continued to evaluate the intactness of the deposits. Vandalized or disturbed deposits were assigned feature numbers, and carefully separated from underlying intact deposits.

In both 1994 and 1995 we managed to reach the much older deposits below a major roof-fall (Table 1; Fig. 3:F45, Fig. 4:F65). If we accept the radiocarbon dates (especially Beta-75875, -90649, -90651), this roof-fall dates between 4300 and 6400 B.C. A more substantial hearth with extremely fired soil was exposed below the roof-fall (Fig. 3:L46/F47). Samples from this feature and other samples below the roof-fall (Beta-75874, -75875, -90651) indicate that occupations extend back to 7500 B.C. Beyond these dates, no other evidence has been found in the 1994–1996 excavations for Archaic period occupations in Coombs Cave.

Above the roof-fall, the absence of substantial features, the thin occupational layers, the infrequency of tools, and the informal nature of refuse disposal (e.g., absence of middens) indicates that occupations were ephemeral and brief. Most artifacts and ecofacts were discarded near where they were used or processed. With one exception (Feature 50), the features are small shallow pits and hearths with little evidence of cleaning and very limited quantities of charcoal.

Feature 50 caps the unit excavated during 1995. Our description elaborates the profile (Fig. 4), because only the southern-edge of this feature is depicted in it. The feature started as a large pit (80 cm diameter and >20 cm deep) excavated down to just above a large sandstone boulder (Fig. 4). The bottom of the pit was lined with several layers of unburned prickly pear pads, ash and charcoal (Fig. 4:F50B). Two sandstone slabs were set vertically into the deposits to create an enclosure within the pit. We believe that Feature 50 functioned as a hearth, because the lower fill within the pit consists of lenses of charcoal, fired sand, and ash. This hearth was probably cleaned-out and reused for considerable time periods during several occupations. Ash and charcoal swept out to the east of the feature (Fig. 4: lensed deposits between F50A and F50B). Some clean-out from this hearth was deposited while the ash and charcoal were still hot, since the surrounding sand exhibits discoloration. Two layers of uncharred grass and pine needles line the upper portion of Feature 50 (Fig. 4:50A). We cannot determine the stratigraphic relationship of Feature 50 to the surrounding deposits because vandals dug into the deposits to the east and to the west of the feature (Fig. 4:F49, 51).

A recent re-examination of Cowboy Cave revealed the existence of pithouses (cf., Jennings 1980, Schroedl and Coulam 1994). Pithouses are known from other caves occupied by Basketmaker and Fremont people (e.g., Matson 1991, Janetski 1993). Feature 50 shares some of the characteristics we often associate with central hearths within pithouses, including vertical slabs. However, we do not believe pithouses were present in Coombs Cave because refuse from cleaning out this hearth was deposited immediately around it, rather than in an external midden, dump, or pit. In addition, the vandals who focused their illegal trenching around the rear of the cave did not expose any slab or juniper-bark lined cists.

Overall densities of lithic artifacts in the 1994 and 1995 units are about average (500 stone artifacts/m^3) for caves on the Colorado Plateau. Occupational events exhibit more than a three-fold increase above the average. Stone artifacts include only a few formal tools, such as projectile points and bifaces, and some chipped-stone debris, mostly small interior flakes from resharpening/finishing stone tools. Ground stone (metates and manos) are extremely fragmentary and have been discolored from use as hearthstones.

A few potsherds are scattered in various occupational levels above the roof-fall. All of them are plain grey-colored sherds, probably from jars. They would usually be classified as Fremont, but recent research on similar ceramics from around the Great Salt Lake indicates that characteristics of plain ceramics may inform us more about human mobility and less about chronological time (Simms et al. 1996).

Such jars, and perhaps the gourds and baskets, may have served as containers to store the water that flows over the rim of the cave (near the oak in Fig. 2) with snow-melt or after rain showers. This runoff served as the major source of water for the occupants of the cave, and limited the extent and intensity of human visitations.

Dating the human occupations in the cave has been frustrating. Based on investigations at other sites, various temporal diagnostics, including arrow points, plain grey ceramics and diverse cultigens, found in the cave date to the second half of the first millennium A.D. These diagnostic artifact occur in most of the occupational levels above the roof-fall. No artifacts have been found in any of our excavations above the roof-fall that date from earlier time periods.

Radiocarbon dates were obtained on pinyon and juniper charcoal from the 1994 field session (Table 2). In 1995 we collected and dated samples of annual grasses. Eight of the 12 samples are from hearths located within what we believe to be intact and stratified deposits, yet nearly all of the dates above the roof-fall are far too old to be associated with ceramics, arrow points and diverse cultigens. Furthermore, the chronological ages of the dates are inconsistent with their stratigraphic order.

The four dates bracketing and below the roof-fall (Beta-75874, -75875, -90649, and -90651) appear to reliably place the age of the deeper deposits as >4300 B.C. Two samples (Beta-90647, -90648) above the roof-fall date as early. Only one sample (Beta-75872) from the 1994 unit and another from the 1994 unit (Beta-90650) date even close to the anticipated age range (A.D. 500-1000) for the deposits above the roof-fall. Four other samples (Beta-75870, -75871, -75873, -90646) dating 825-2925 B.C. are also believed to be too old.

In the absence of any evidence from our excavations beyond the dates for Archaic occupations in Coombs Cave, two alternative explanations are offered for the discrepancies in the radiocarbon dates: (1) the deposits are far more disturbed by the vandals than we recognized; or (2) organic materials introduced into the cave during earlier occupations were reused by later occupants. We believe the following review of the evidence supports the second explanation.

In order for vandals to have introduced the much older wood and charcoal into the upper deposits required them to dig through the roof-fall. Examination of vandal pits in and adjacent to our units has shown that the roof-fall posed as much of a problem for them to penetrate as it has for us. We have yet to find any clear stratigraphic evidence that the vandals ever dug completely through or below the roof-fall.

Table 2. Radiocarbon dates from the 1994 excavation unit in Coombs Cave (42GR383). Calibrations provided by Beta Analytic.

Lab (Beta-)	Feature number	Conventional C14 age (B.P.)	Calibrated age 2 sigma	Type of feature
(A) 1994 unit (1): Wood charcoal samples				
75870	4	2820±60	BC 1130–825	Hearth
75871	17	4270±50	BC 2925–2705	Hearth
75872	25	1790±50	AD 120–390	Hearth
75873	40	3820+60	BC 2460–2040	Hearth
	----- major roof-fall event with occupation hiatus -----			
75874	46	8220±80	BC 7450–7020	Layer
75875	47	7880±80	BC 7015–6480	Hearth
(B) 1995 unit (2): Wild grass samples				
90646	50	3130±80	BC 1530–1170	Hearth
90647	50B	5300±70	BC 4325–3970	Hearth
90648	59	6540±110	BC 5605–5260	Hearth[a]
90649	61	6140±90	BC 5440–5260	on roof-fall
90650	64	1180±40	AD 775–975	on roof-fall[b]
90651	66	7620±60	BC 6495–6365	below roof-fall[b]

[a] Some twigs in the sample.

The presence of numerous intact cultural features, which also were the source of many of the radiocarbon samples, argues against attributing the confusion in the dates simply to vandalism and misreading the stratigraphy. Feature 50, in particular, capped much of the deeper deposits excavated in 1995.

We believe the evidence supports the second alternative explanation--later occupants recycled organic materials introduced into the cave at earlier times. After an initial occupation during the Archaic period, a major roof-fall occurred within Coombs Cave which coincides with similar roof-falls and occupational hiatuses (4000-2500 B.C.) in other caves on the Colorado Plateau and Great Basin (Beck 1995:229– 230). Based on the time diagnostic artifacts and two of the eight radiocarbon above the roof-fall, occupation resumed in Coombs Cave during the first millennium A.D. We propose that the six older samples from above the roof-fall represent older grass and wood burned in later hearths. This older wood and grass probably came from below the roof-fall. With the exception of Feature 50, we have found little evidence for early inhabitants digging into earlier deposits within Coombs Cave.

Both explanations leave us puzzled about how later visitors to the cave managed to obtain older wood and grass from below the roof-fall. It is possible that the older organic materials were poorly buried and lay exposed along the steep slope at the front of the cave. We believe it is less probable that organic material was ejected at the time of the roof-fall.

The cave's true value to archaeology lies in the abundant and varied plant remains brought into the cave by its occupants. They include corn, gourd, beans and squash, many kinds of grasses, juniper, yucca, sunflower, onion, and pinyon pine nuts.

Two major groups of plant remains occur within the cave: (1) cultigens (domesticated plants such as corn, beans, squash, gourds)--indicative of at least a partial agricultural life way; and (2) non-cultigens--indicative of a life way more dependent on hunting and gathering wild species. Statistical analysis of the quantities and densities of these remains, accomplished after the 1994 field season, shows quite clearly that the two groups vary independently. Layers abundant in cultigens also have fewer non-cultigens. Figure 5 graphs the amounts of corn, pinyon pine nuts, and various grasses. While pine nuts and grass peak together, corn peaks in layers without these wild resources, with one early exception.

Correlations among other remains add support to our contention that the cave was being used at times by people relying on foraging for wild species and at other times by the same people relying upon grown crops. For example, nonhuman animals may have introduced unburned bones (birds, carnivores, rodents) along with bones from humans uncooked food or food prepared in ways that did not char the bones. We can attribute most burned bones to humans, although some bones may have been accidentally charred due to

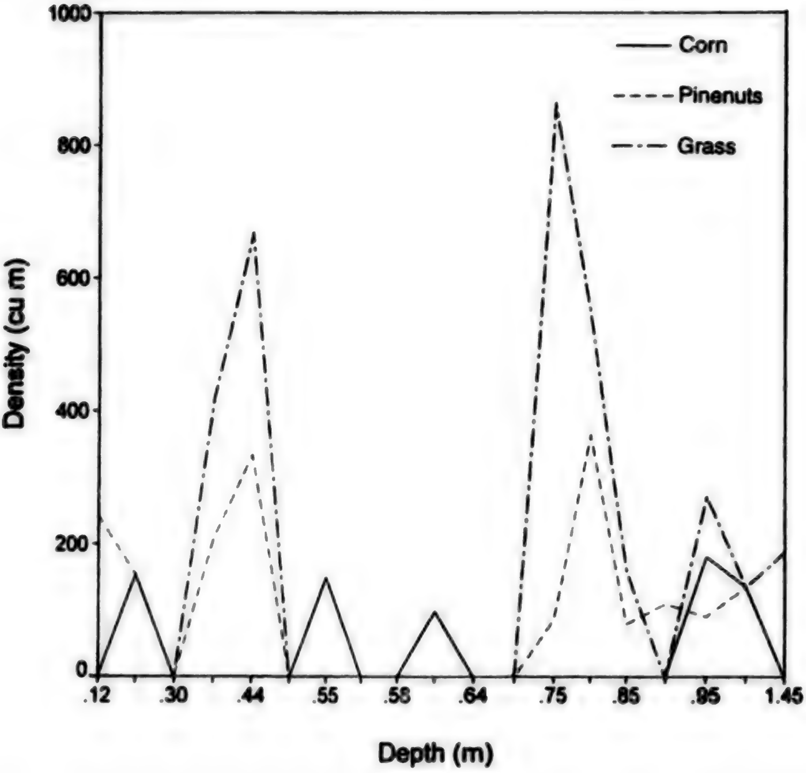


Fig. 5. Densities of corn, pine nuts, and grass within the 1994 excavation at Coombs Cave (42 GR383).

their proximity to hearths. We would expect burned bones to be more numerous in the layers resulting from occupations oriented toward non-farming activities. Unburned bones occur in various layers throughout the 1994 unit, but burned bones occur most frequently in layers with higher densities of non-cultigens (Fig. 6). Wild grasses, burned bone and pine nuts peak together.

Discussion

We have no reason to believe that the same people did not continue to visit and use this cave at various times as hunters, gatherers, or as farmers. The cave was used in different ways as the focus and/or success of the

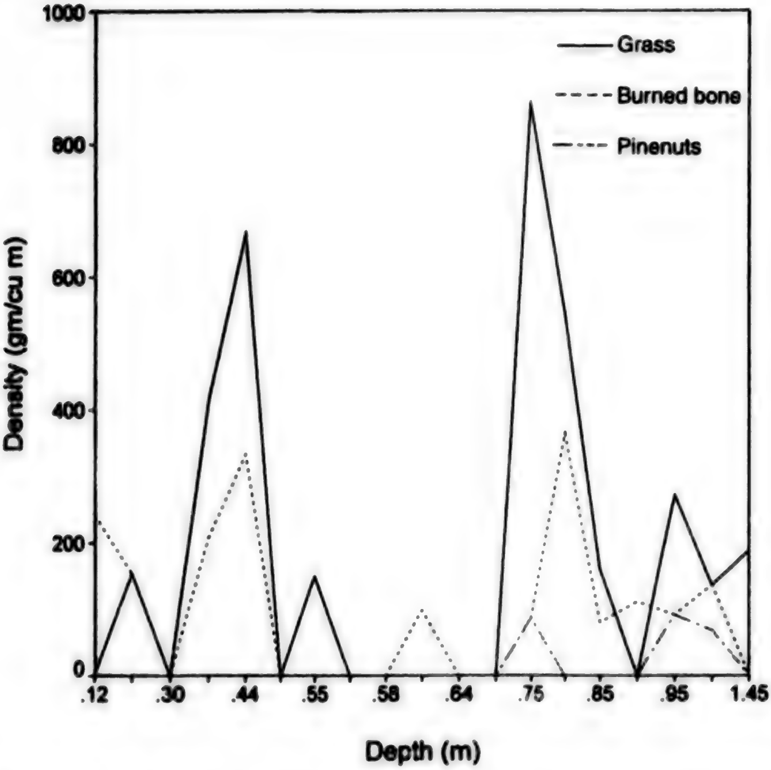


Fig. 6. Weights of grass, burned bone, and pine nuts within the 1994 excavation at Coombs Cave (42GR383).

subsistence strategies varied. Farming was probably only successful during the brief periods of warmer climatic conditions with a longer growing season.

At this elevation, farmers consistently ran the risk of losing their crops to early or late frosts. Furthermore, the cultigens represent primarily successful crops. Farmers whose crops failed may be responsible for the layers without cultigens when they resorted to gathering and hunting wild species. By refining our analysis and using insights from middle-range theory and ethnoarchaeology, we may be able to distinguish between these alternatives in the archaeological record.

In this portion of the Colorado Plateau: Once a farmer, not always a farmer. No single transition to farming is apparent, instead switching back and forth between the use of domesticated cultigens and wild species continues throughout the levels above the roof-fall.

The field and cave are 5.6 km from permanent water (Fisher Valley). Even with the use of runoff water collected under the rim of the cave, the absence of more substantial water sources closer to the field and cave contributed to the brief and episodic use of this portion of the Colorado Plateau.

The rock alignments in Coombs Field retained and spread water across the sandy ridge between two major washes. Sandy deposits accumulated behind the alignments, increasing the amount and quality of arable land.

Substantial fields, incorporating various water control features, are known from other portions of the American Southwest at higher elevations in areas experiencing population pressure (e.g., Maxwell and Anschuetz 1992, Lightfoot and Eddy 1995). Coombs Field differs from most of these because it is not located near an agricultural village. The evidence from Coombs Cave suggests ephemeral and brief occupations by small groups of mobile people who created and used Coombs Field. We believe that this evidence suggests that the inhabitants continued to be mobile egalitarian people, even when they were farmers.

After their initial labor investment to construct and clear their field, very little further maintenance was required. The growth of oak and other vegetation stabilized the rock alignments, and furthered the accumulation of sediments behind them.

The use of this field and the associated cave is presumed to have been linked with the growth of more substantial villages in Fisher Valley, a north-flowing tributary of the Colorado River. These former villages are 5.6 km west of the cave and field, but have not been investigated by professional archaeologists, in part because they lie on private land.

The existing survey data from the region are inadequate for addressing questions about demographic change and population pressure in the lower-elevations along the Colorado and Dolores River (Fawcett 1994). Chronological resolution is also insufficient to permit this kind of analysis. We cannot address these questions until a well-designed sample survey is completed that includes both the mesas and valleys.

Conclusions

We have partially excavated a large dry cave containing remarkable amounts of ecofacts, including many cultigens, but little artifactual material. The human use of this cave was linked to nearby agricultural field where at least nine linear rock alignments were constructed to control and spread water within the field. Coombs Cave exhibits episodic and ephemeral use over several centuries (ca. A.D. 500–1000). Taken together these sites suggest an alternation between two extremes of a subsistence continuum: farming domesticated plants and foraging for wild plants and animals. At this location, we have an excellent opportunity to study fluctuations in reliance on agriculture under marginal conditions with an extended time window.

Climatic changes effecting agricultural success may have contributed to the recurrent switching between farming, hunting, and gathering by the creators and users of the field and cave. Yet little evidence exists to suggest that the sites were visited on more than a seasonal basis by egalitarian people. Social and political tensions being negotiated among various human groups may also have contributed to the attempts to farm at this marginal location.

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